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ARTHUR H. PIERCE, SMITH COLLEGE (*Bulletin*)

On the Functions of the Cerebrum: the Occipital Lobes.

Shepherd Ivory Franz, Ph.D.,

Research Assistant of the Carnegie Institution of Washington;
Scientific Director and Psychologist, Government Hospital for the Insane;
Professor of Physiology, George Washington University.

with the coopération of

Gonzalo R. Lafora, M.D.,
Histopathologist, Government Hospital for the Insane.

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1928

Wife

Dr. Franz

INTRODUCTION¹

The positive statements regarding the functions of the occipital lobes might lead one unacquainted with the facts to believe that the functions of these portions of the cerebrum were well understood. A careful consideration of the experimental and clinical phenomena accompanying disturbances in these areas does not support the general belief, and although they are among the first parts of the brain to have been investigated by physiological methods there remains much to be done before we may say we understand their function and their method of working. We may apply directly to this region of the cerebrum the statement of Hitzig, made a decade ago in regard to the whole brain: "Die Hirnrinde und ihre Zusammenwirkung mit ihre subcortikalen Centren stellen vielmehr noch heute einen dunklen Continent vor (31)." That to some extent and in some manner the cortex in the occipital portion of the brain functions in connection with the retinae is probably true, but how it functions and in what manner it is connected with the retinae have not been determined

¹ The present work was made possible by a grant from the Carnegie Institution of Washington to the author as research assistant. This assistance is hereby acknowledged and the author expresses his sense of obligation for it. On the histological side of the work the author has had the opportunity of the coöperation of Drs. N. Achúcarro and Gonzalo R. Lafora, respectively former and present histopathologist at this institution. Assistance in the observation and in the training of the monkeys has been given especially by Dr. A. H. Sutherland, formerly of this institution and now of the University of Illinois, and by Drs. Achúcarro, Barnes, Blackburn, and Lafora and their assistance is hereby gratefully acknowledged.

The present work deals mainly with the lateral portions of the occipital lobes, and it is expected that articles will appear later dealing with the mesial aspect and with the results of electrical stimulation.

While this article was in manuscript form there appeared von Bechterew's *Ueber die Funktionen der Nervencentra*, which contains a resumé of much work on the occipital lobes. Von B. discusses to great length the work of Goltz, of Munk and of Luciani but slights much which is discussed in pp. 9-23.

to the complete satisfaction of those who have most carefully investigated the matter.

The numerous recent histological studies of the architecture of the cerebral cortex emphasizes the fact that the clinical and physiological problems of the localization of function are not simple, either in method or in interpretation. Although there is considerable diversity in the results of the different histological investigators, there is, on the other hand, sufficient uniformity to indicate that the old landmarks of the cerebrum must be given up and that the facts must be viewed in connection with the plans made by recent surveys. Most of the fissures, especially those of a secondary character, are of little value for the limitation of special areas, and it is necessary at the present time to consider the areas from an entirely different standpoint. This standpoint is the intimate structure of the cortex, the number and grouping of the cells, the arrangements of the fibers, and the combination of these. It has been shown that we may almost entirely disregard the cerebral fissures and divide the cortex of the cerebrum into approximately fifteen areas, each with an histological structure quite distinct and different from those of the surrounding areas.

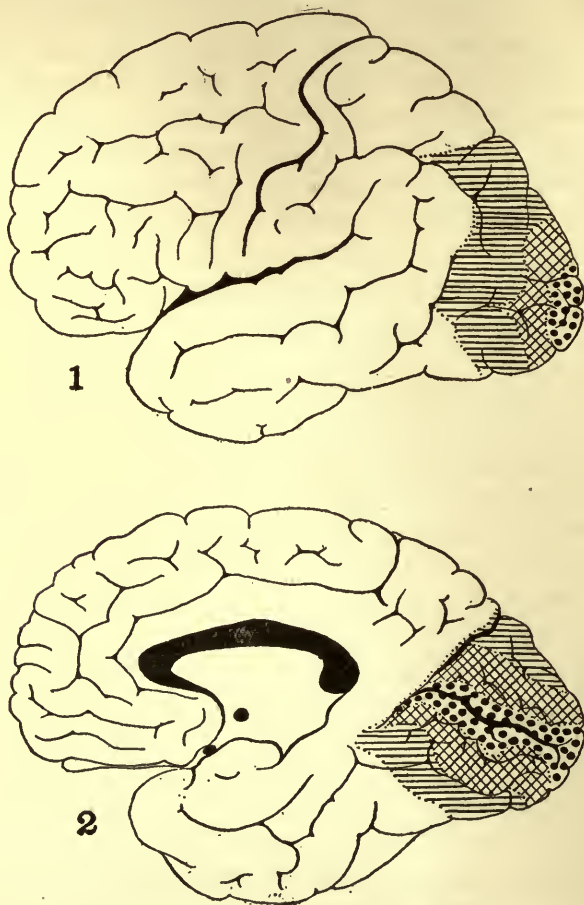
The histological studies have led to the formulation of hypotheses regarding the probable function of the parts and the statement is made that each of the areas histologically distinct is also physiologically different from the bordering areas. Although all the histologists appear to give to their results an interpretation more or less physiological, Brodmann (9, 10) in particular has expressed this stand more plainly and more positively than most of the investigators. He has written: "Es scheint doch näher zu liegen und vom histologischen Standpunkte aus geradezu geboten, spezifisch differenten Rindenzellen auch qualitativ differente Funktionen zuzuschreiben;" and in a further discussion of the matter: "Die spezifische histologische Differenzierung von Rindenarealen beweist unwiderlegbar deren spezifische funktionelle Differenzierung" (9). This leads directly to the anatomical division of cerebral function, to a sort of phrenology, and to an anatomy of mind which will not bear criticism.

THE OCCIPITAL LOBE

The gross appearance and the extent of the occipital lobe may be learned from the text books of anatomy (61), or will be recalled by a glance at figs. 1 and 2. The lobe comprises about one-eighth of the superficial part of the cerebral cortex. On the mesial aspect of the hemisphere the calcarine fissure is included in this area, and its upper and anterior limits are roughly fixed by the parieto-occipital sulcus. On the lateral aspect it reaches to the transverse occipital fissure. In the fresh as well as in stained sections of part of this region there can be seen in the cortex without the aid of the microscope a distinctly lighter streak, apparently dividing the cortex into two layers. This is the line of Gennari which, both macroscopically and microscopically, gives to this area an appearance very different from all other parts of the cerebral cortex.

Further examinations of the cortex by histological methods reveal other differences. The larger region is found to have two or three different types of arrangements of cells and fibers, so that by the more careful methods it is possible to distinguish and to differentiate two or three areas of anatomically (histologically) distinct types. The most characteristic of these areas is the one in which the line of Gennari is prominent, an area which may be called the calcarine area. This area surrounds the calcarine fissure, and in man reaches beyond the occipital pole toward the lateral aspect of the cerebrum for only a very short distance. The limits of this area have been accurately determined by a number of investigators, all of whom report essentially the same results. The structure of this region is described by Campbell as follows (11, p. 17): "The characters which distinguish the calcarine type of cell lamination are, first, the almost unique layer of large stellate cells usurping the position occupied by the external layer of large pyramidal cells in other regions; secondly, the existence of pale-stained zones above and below the uncommonly well-marked layer of stellate cells, the upper of which marks the position of the line of Gennari; thirdly, the presence in the depths of the cortex of the layer of solitary cells of Meynert, cells which differ from homonymous cells in any other part of

the brain." The remainder of the occipital lobe is considered by Campbell to be one area, while Brodmann has been able to distinguish two separate areas, which he admits are closely related (10, p. 228). The cortex surrounding the calcarine area,

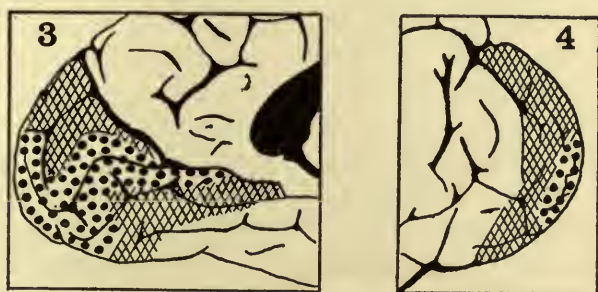


FIGS. 1 and 2. The human cerebrum, with the areal differentiation of the occipital lobe. The dotted part is the calcarine type, and the parts marked by horizontal lines and by cross hatching are the remainder of the so-called visual cortex. Adapted from Brodmann, and reduced.

and extending 1.5 to 2 cm. beyond it, is supposed to have a function somewhat similar to that of the calcarine area, in that it is intimately related to the calcarine area, and has been correlated

with certain clinical findings relating to vision. To this region Campbell gives the name visuo-psychic as distinguished from the calcarine which is called visuo-sensory.² The structural appearance of this surrounding area is somewhat similar to that of the calcarine area, but sufficiently different from the latter to be considered distinct. The cortex is of greater depth, the plexiform and small and medium-sized pyramidal cells are all appreciably deeper, but the latter two are less numerous; the large pyramidal cells are mixed with the other cells and do not form a layer by themselves; the layer of stellate cells has an appearance similar to that in the calcarine area, and the other cell elements are not divided into layers as in the calcarine region.

Figs. 1 and 2 illustrate the division by histological methods of the occipital cortex in man by Brodmann. Here is shown the



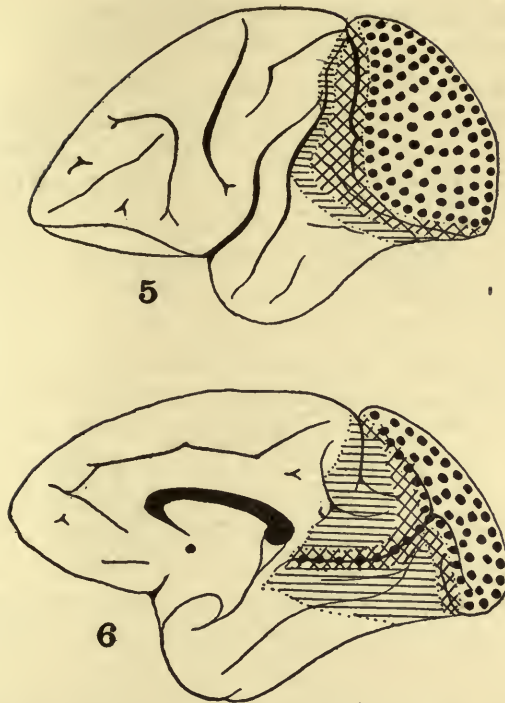
FIGS. 3 and 4. The occipital pole of the human cerebrum, with the areal distributions of the so-called visuo-sensory and the visuo-psychic regions. The dotted portion is the calcarine type of cortex, and the cross hatched portion is the visuo-psychic area. Adapted from Campbell. 3, the mesial aspect; 4, the lateral aspect.

calcarine area, marked by large dots, surrounding that fissure, and in the neighboring regions the two areas closely related to the calcarine but differing from the latter in cell and fiber structure. The two areas, as has been indicated above, are not absolutely distinct and have been grouped by Brodmann to make one area. By this grouping Brodmann closely approaches the divisions made by Campbell (11), by Elliot Smith (69) and by Bolton (8), as well as those made by the earlier investigators.

² These names were previously used by Bolton.

The division of the cortex by Campbell is given in figs. 3 and 4, which should be compared with the division by Brodmann in figs. 1 and 2. It will be seen that the total extent of the cortex supposedly devoted to visual function is approximately the same in the two figures, the apparent difference being accounted for by the different views of the brain which the two investigators have used for the delineation of the areas. The most marked difference between the areal distributions of Campbell and Brodmann is the larger relative size of the calcarine cortex outlined by Campbell. The surrounding region is, however, not so easily differentiated from the remainder of the brain as is the calcarine cortex, and the variations of the individual observers may be due to actual differences in material, as Bolton (7) suggests in regard to another matter. Bolton reports that in an examination of brains for the exact localization of the visual cortex he found individual differences apart from the age and the visual abilities of the people whose brains he examined, and he remarks that "as such differences exist in a projection area, it is possible that more marked variations will occur in the case of the later specialized areas of different brains" (7, p. 309).

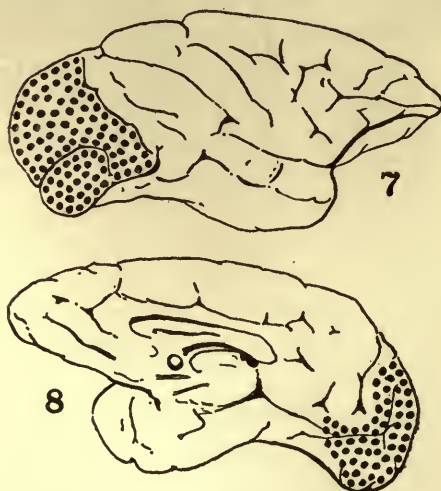
In the monkey the occipital lobe is more constant and more easily mapped out by fissures than in the human brain. It may be described as that part of the cortex on the lateral aspect almost inclosed by the parieto-occipital and the inf. occipital fissures, and as the part on the mesial aspect which surrounds the calcarine fissure, bounded above by the parieto-occipital fissure and below by a line drawn from the calcarine fissure to the inferior occipital. The cortex in this area shows types of arrangement similar to those found in the human brain, and it has been found possible to map the region into at least two distinct areas, the so-called visuo-sensory and the visuo-psychic. Figs. 5 and 6 show this division, but into three areas corresponding with the three divisions of the human brain by Brodmann. It will be seen that the calcarine type of cortex occupies a much larger area than in the human brain, not only relatively to the size of the whole cortex, but also absolutely larger than the same type in man if we disregard the infolding of the calcarine fissure. Brodmann has



FIGS. 5 and 6. Distribution of the various types of cortex in the occipital lobe of the monkey (*Cercopithecus*). Same designations for the areas as in figure 1. Adapted from Brodmann, and reduced.

not illustrated the extent of this area in the Macaque monkey, but only in the *Cercopithecus*, the brain of which closely resembles that of the Macaque. Mott has given illustrations of the Macaque brain with the distribution of the calcarine type of cortex, which are here reproduced (figs. 7 and 8) for comparison with that of the distribution in the *Cercopithecus* by Brodmann. The findings of Mott (50) differ very much from those of Brodmann in the allied family. He does not illustrate the extension of the so-called visuo-psychic type of cortex and it is, therefore, impossible to make a full comparison with the findings of Brodmann. It may be said, however, that the examination of the brains of the Rhesus monkeys used in the present work has shown a distribution of the calcarine type of cortex more nearly like that

found by Brodmann in *Cercopithecus* than that illustrated by Mott in the Rhesus.³



FIGS. 7 and 8. Illustrating the distribution of the calcarine type of cortex in the Macaque monkey (*Macacus Rhesus*). Adapted from Mott, and reduced.

From the resumé of the work of the different histologists it will be seen that the occipital cortex can be roughly divided into two areas, of somewhat different structure, and that one of these areas is very definite. The anatomo-pathological studies indicate a close connection between the occipital lobes and the eyes and this connection is admitted for the calcarine type of cortex more generally than for the surrounding regions. In the next section of this article, we shall see there is little warrant for the assumption that the cortex surrounding the calcarine type of cortex has visuo-psychic functions, although most workers in this field believe that the calcarine cortex is concerned with visual sensations.

The occipital lobe is in connection with the external geniculate bodies, the pulvinar and the anterior corpora quadrigemina.⁴

³No special effort was made to mark the limits of the other areas of the occipital cortex and a definite statement of their extent in the Rhesus monkey can not be made at present.

⁴For the description of the relations and the connections between the occipital lobes and the retinae, see especially von Monakow (45, 47 and 48), Dimmer (13), Knies (38), Moeli (44), and Mott (49).

THE LOCALIZATION OF FUNCTION IN THE OCCIPITAL LOBE

Movement. Electrical stimulation of the occipital cortex results in movements of the eyeballs and of the intrinsic eye muscles. The eyeball movements are associated movements. Different observers have located in this region centers for a number of movements, and have demonstrated a functional connection between this region and the precentral cortex. It has been found that the eye movements occur upon stimulation of the occipital lobes even after the frontal cortex has been destroyed, and that they also occur upon stimulation of the frontal cortex after the occipital lobes have been extirpated. This has been taken to mean that there are independent centers for the movements of the eyes; one in the occipital lobe, the other in the cortex anterior to the central fissure.

Ferrier (14) reported that in monkeys stimulation of points on the angular gyrus produced movements of the eyes "to the opposite side, with an upward and downward deviation, according as the electrodes are placed" anterior or posterior to the parallel fissure. He has also noted the contraction of the pupils and the tendency to closure of the eyelids, and occasionally an associated movement of the head to the opposite side. Ferrier's observations have not been confirmed by other observers, and Schäfer (62, 64) and others assign to the occipital lobes this motor function. Schäfer reports: "If the electrodes are applied directly to the upper surface of the occipital lobe, conjugate deviation to the opposite side with downward direction of the visual axes is extremely well marked, and it is also produced by excitation of the upper part of the mesial surface of that lobe, and of the quadrate lobule immediately in front of the internal parieto-occipital fissure. If, on the other hand, the posterior extremity of the occipital lobe, its lower or tentorial surface, and the posterior and lowermost part of its mesial surface be stimulated, the lateral deviation is combined with an upward movement. In both cases the downward or upward movement may be almost uncomplicated by lateral deviation; this depends upon the position of the electrodes. On the other hand, there is an intermediate zone, narrow on the mesial surface of the lobe, and broader upon the outer or convex surface, excitation of which

is productive of simple lateral deviation. All the effects are strongest upon the mesial surface, especially toward the anterior limit of the lobe; it is here that the local point for the movements is located." On the assumption that the eye movements resulting from stimulation of the occipital lobes are due to something akin to sensations Schäfer (64, p. 5) was led to conclude that the occipital lobe has the following physiological connections: "The whole of the visual area of one hemisphere is connected with corresponding lateral half of both retinae. The upper zone of the visual area of one hemisphere is connected with the upper part of the corresponding lateral half of both retinae. The intermediate zone of the visual area is connected with the middle part of the corresponding lateral half of both retinae." Von Bechterew (2) has located only three centers for movement of the extrinsic eye muscles, and he has reported that eye movements may be obtained from stimulation of the parietal lobe as well as from the stimulation of the occipital. It is worthy of note that Steiner (70) has found the occipital lobe unresponsive at birth, although at this time the stimulation of the frontal (pre-Rolandic) cortex results in eye movements. This has been confirmed by Berger.⁵

Many observers have recorded movements of the iris, i. e., pupillary changes, following the stimulation of the occipital lobes. Von Bechterew has located in the occipital lobes two centers for pupillary movements, a contraction center in the middle part of the occipital lobe, and a dilating center slightly inwards from the contraction center. These results or similar ones have been found by other observers, and they are partly confirmed by the observations on man when there is disease or destruction of the occipital cortex.⁶

The observation of Schäfer (66, p. 750) on the latent periods of the movements from stimulation of the occipital lobe and of the precentral cortex are of primary importance, and have often

⁵ See also Schäfer (62), Gerwer (22), Mott and Schäfer (51) and Obregia (57).

⁶ On the pupillary changes see also the following articles: v. Bechterew (2, 3); Parsons (59); Mislowsky (43); and also Alamagny (1); zur Verth (72); Bernheimer (6); Leyden (39).

been overlooked by other investigators. He has carefully timed the movements and finds that the latent period for movements from occipital lobe stimulation is much longer than that from the stimulation of the Rolandic area. That this lengthening of the time is not due to the passage of the impulse to the frontal lobe, i. e., to the motor cortex, and thence to the muscles is shown by the fact that the movements from stimulation of the occipitals may be obtained after the frontal lobes have been excised. We are, therefore, compelled to conclude that the cells in the occipital lobes have a more direct connection than that through the motor cortex, although it is apparent from the results of Schäfer's work that there are more intercalated cells in the chain from the occipital lobes to the eye than from the pre-Rolandic cortex to the same muscles.

Sensation. It was known for a long time that destruction or injury of parts of the cerebrum caused visual defects or disturbances, but the recognition of a localized center or centers for visual sensation and perception has been largely due to the results of experiments on animals. In the hands of different observers the method of extirpation has led to somewhat discordant results, and to opposing conclusions. The controversies regarding the functions of the occipital lobes will not detain us here, but although they apparently did not change the opinions of those who took leading parts therein they have left us many observations of value.

Extirpation of certain cortical areas in the dog's brain led Munk to the conclusion that in this animal there is a center (designated by him as A1) for visual perception and that the surrounding more extensive region was a subsidiary visual center which could be used when the primary center was injured or destroyed. Munk (52-56) furthermore attempted a more careful localization and attributed to parts of the center more definite functions. The conclusions of Munk were strongly combatted by Goltz who ^{the} at first denied there was any localization in the cortex of the brain, but who later admitted that a certain amount of localization was possible, and in fact was indicated by the results of the experimental investigations. The position taken

by Goltz (23-25) in regard to localization of vision was that although a visual defect, which he did not deny, might be produced by the ablation of part of the cerebral cortex, the defect was not due to the extirpation of the cortical cells concerned with the visual processes, but to a general effect and might be produced by the extirpation of parts of the brain other than that assigned the visual function by Munk. Regarding this he has written: (23) "Indem ich also auf Grund meiner neueren Erfahrungen einen grösseren Einfluss des Hinterhirns auf das Sehvermögen für festgestellt erachte, kommt es mir dabei nicht in den Sinn, etwa eine begrenzte Sehsphäre zuzugeben, wie sie Ferrier, Munk und Luciani konstruiert haben." This admission of the possibility of localization is much the same as that of Loeb (40-42) who investigated the so-called visual cortex at a later date, and who has taken a stand much like that of Goltz. Loeb asserts that the visual disturbance following operations upon the occipital lobes which is temporary in character is due to a lowering of the irritability of the retina-cerebral cortex mechanism. The differences between the Munk and Goltz school does not, however, disappear even if we consider that the Goltz and Loeb explanation of the latter be correct for the symptoms that are temporary. Part of the difference between the explanations of Munk and Goltz rests, as von Monakow has shown, upon different standpoints in the collection of the data. Goltz has used as evidences of the presence of visual sensations the movements of the eyes and of the related parts when the eyes are stimulated by light, but there is no reason to believe that these reactions are more than reflex in character, and there is good reason to believe that they do not depend entirely upon the activity of the cerebral cortex. It would be equally correct to say that there was no localization of movement or of the skin sensations because it is possible to get reflexes of the leg after there has been complete separation of the spinal cord from the cerebrum. Loeb does admit, however, that the destruction of the occipital lobe in man is followed by a blindness, which he believes is due to a loss of irritability on one side of each retina, but he explains the results in dogs to be not a loss but only a decrease

in irritability in that organ.⁷ He furthermore asserts that, with Goltz, he believes the associative memory of animals deprived of their occipital lobes does not differ from that they had previous to the operation. The main difference between Goltz and Loeb and the followers of Munk, Hitzig, and others, is in the conception of the relation of the brain to mental processes. The former object to the interpretation that extirpations of or injury to parts of the brain cause psychical disturbances, while Ferrier, Munk, Hitzig, and other investigators interpret the defects to be psychical. From the standpoint of localization, which apparently all admit in some form, the important question is not concerning the presence or absence of certain psychical disturbances but the definite or indefinite restriction of certain functions to certain areas. There can be no doubt that in man certain cerebral destructions produce certain effects of the nature of loss of associations, e. g., those of speech, and the clinicians still debate whether or not these losses mean mental deterioration. Whether or not the disturbances are to be interpreted as psychical will depend upon the connotation of the word psychical. ✓

The conclusions of Munk were supported by von Monakow (46) both from the results of personal experiments and from the examination of the brains of animals upon which Munk had operated. von Monakow, however, believes the visual area is not as small as it was pictured by Munk, and considers that, in dogs at least, it extends anteriorly beyond the limits assigned by Munk.

The conditions reported by Hitzig (30-34) following removal of parts of the occipital lobes in dogs was that of crossed amblyopia. This is unlike the results of other investigators, who have reported a condition of hemianopia (for the opposite visual field) following the extirpation of cortical regions in both dogs and monkeys. Hitzig had also been led to conclude that a similar condition may follow lesions of the anterior part of the brain, but these results have not been confirmed by independent investigators. As an explanation of Hitzig's conclusions it has been pointed out that the visual defect in the dog following the extir-

⁷ Why he has selected the eye in this connection is not made clear, for it would seem that the explanation should be made in regard to the central nervous structures.

pation of one occipital lobe is blindness, not for the opposite eye, but for objects in the opposite field of vision, which on account of the large number of the optic fibers crossing at the chiasm is more marked (i. e., includes more than half of the visual field) in the opposite eye in the dog. Perimetric examinations of animals have shown that from two-thirds to three-quarters of one retina in the dog is connected with the homonymous occipital lobe. The conclusions of Hitzig are, therefore, taken to indicate that on account of the involvement of such a proportion of the retina of the one eye by an unilateral occipital lesion the exact nature of the defect was not discovered, i. e., there was retention of vision for only about one-quarter of the field and the appearance was that of a complete blindness for the whole field of that eye.

Using monkeys as subjects, Ferrier localized the visual area at first in the angular gyrus, but later concluded that the occipital lobe was used in connection with the angular gyrus, and called the area the "occipito-angular" area. The later conclusions of Ferrier were due to the criticism of his early work by Schäfer and others, and to the fact that he repeated the work using somewhat different methods. His early experiments were performed without aseptic precautions, and it is this condition and its resultant consequences (e. g., the secondary extension of the injury by infection, etc.,) which Ferrier uses to explain his first results and conclusions. In the later localization work by Ferrier (14, p. 268-305) the angular gyrus is given a prominent place and he reports that the occipital lobes may be cut away alone without appreciable impairment of vision. The visual defect reported by Ferrier (14, p. 273) was that of amblyopia. Many of the animals operated upon by Ferrier showed a blindness which persisted for only a few hours. This has been urged by others as a criticism of Ferrier's work and conclusions, for it has been said that the observations taken so soon after the completion of the operation do not warrant the conclusion of blindness. Although Ferrier rightly retorts that the "period of reliable observation is not to be measured by the mere time that has elapsed since the operation, for the period of recovery is most variable, many animals being up and active almost before their wounds have been

dressed," it does appear to stretch a point to conclude that the blindness may remain for only a few hours and then entirely disappear. In reply to Schäfer, the citation of cases from his work in 1884 is not convincing in regard to the part played by the angular gyrus in visual perception or sensations (15).

Following are abstracts of several cases cited by him in the discussion with Schäfer: In one monkey the left angular gyrus was cauterized. The left eye was secured so that the animal could not use it for vision. A half hour after the operation the animal was apparently "wide awake but would not move unless touched"; it sprawled on the floor and knocked against obstacles; an hour later it bounded away when it was touched and ran against the leg of a table, but did not show signs of perception when it was approached cautiously without noise; on the following day "no defect of vision, amblyopic or hemiopic, could be detected." In regard to the effects of similar lesions on other animals he says: "Similar results were obtained in many other instances, and if in some they were even more transient, this may have been due to less extensive destruction or perhaps differences in animals as to the relative importance of this region in the ordinary exercise of their visual function." Three cases cited by him are to be compared with the results in the present work. In these three animals the occipital lobes were destroyed or severed with great care so that the angular gyri were not injured. In one the occipital lobes were exposed and the surfaces were "destroyed by cautery, which was also passed deeply into the interior of the lobes so as to cause as much disorganization as possible. Care was taken not to injure the angular gyrus." About forty minutes after the operation the animal began to move but staggered a good deal; its eyes were open and the pupils were dilated. An hour and a half later there was "emphatic evidence of sight; ran away as I approached it, carefully avoiding obstacles"; it entered its cage, and avoided a cat that had taken up its quarters there; "tried to escape my hand when I offered to lay hold of it, but picked up a raisin which I had left on the perch." In a second animal the occipital lobes were severed "by a perpendicular section with hot wires about a quarter of an inch posterior to the parieto-occipital fissure, so as to avoid all inter-

ference with the angular gyrus;" in twenty-five minutes, it was observed that the animal "can see quite as well, as it avoids obstacles, and when removed, regains its position by the fire." In a third animal "both occipital lobes were severed with a galvanic cautery and scooped out bodily; the line of incision in both cases passed between the anterior extremity of the first occipital and the parieto-occipital sulcus;" in half an hour the animal sat up and wanted to move about; for two hours there were no definite tests of vision, but at the end of that time "a piece of apple was thrown into the cage, and though it fell a full arm's length away, the animal, without the slightest hesitation or want of precision, put forth its left hand, picked it up and ate."

Ferrier explains the results of Schäfer and of Munk on the ground that both of these investigators cut away more than the occipital lobes and that in their experiments the angular gyri were injured. The greatest difference, however, between the conclusions of Ferrier and Schäfer is that the latter believes the blindness is of the nature of an hemianopsia. The results obtained by Schäfer, especially those in conjunction with Sanger Brown, are apparently convincing not only in regard to the participation of the occipitals in vision, but also in regard to the character of the defect following lesions in these regions (67). Schäfer (63, 65) not only obtained results on the occipitals opposed to those of Ferrier but has failed to obtain the positive results on the angular gyri reported by Ferrier to be constant. In fact, Schäfer has shown that the angular gyri may be removed without interfering with vision in the least, but that when these parts are removed and the underlying fibers (going to the occipital lobes) are injured, some visual disturbances are to be noticed. Some of Schäfer's results are particularly instructive. One animal upon which he operated, extirpating the angular gyri on both sides, showed no loss of vision, no defect of movement of the eyes, and no anesthesia of the conjunctiva or the cornea, and although this animal was kept alive for several months, no disturbance of the eyes, visual or otherwise, was found. In this connection Schäfer concludes: "A single well marked negative case like this is conclusive against the idea that in the monkey cerebral visual perceptions are localized in the angular gyri" (63, p. 365). On the

other hand the positive results following extirpations of the occipital lobes are worthy of note. One animal, the left occipital of which was completely removed showed a bilateral homonymous hemianopsia, persisting for the whole time the animal remained alive (eight months) (63, p. 367). Another monkey from which both occipitals were removed showed a "total and persistent blindness. The animal could only find food by groping and smelling. Brought into a strange place, it ran against every obstacle. Placed in a dark room and with a light flashed upon it, no signs of perception were given. Hearing was very acute and all other senses besides vision were unimpaired" (63, p. 368-9). This animal was clinically in the same condition as a monkey observed by Ferrier and Yeo, from the brain of which they removed both occipitals and both angular gyri. Other cases were cited which confirm this general conclusion of the non-participation of the angular gyri in the same sensory processes. In conclusion Schäfer says that for complete blindness the "removal of the lobe must be complete and when a small portion of one of the lobes is left, although blindness is not complete, yet the limit of the visual field of the retinae may be greatly restricted" (63, p. 370).

Schäfer sums up the differences between him and Ferrier as follows: "The chief points at issue are (1) the connection of the angular gyrus with central vision of the opposite eye; (2) the relative importance of the occipital lobe. According to Dr. Ferrier's experiments, decortication of the angular gyrus of one side produces blindness of the opposite eye (amblyopia); of both sides produces blindness of both eyes. According to our experiments, decortication of the angular gyrus of one or both sides is not necessarily followed by any visual defects perceptible to our means of investigation in animals; but complete eradication of the gyrus produces hemiopia (not amblyopia), which is temporary only. According to Dr. Ferrier's experiments, destruction of one or both occipital lobes alone produces no appreciable effect whatever on vision. According to our experiments—which are merely confirmatory of those of Munk—removal of the occipital lobe only, without the angular gyrus, produces permanent hemiopia; of both occipital lobes, blindness of both eyes

which is also permanent and, so far as we were able to judge, complete" (65, pp. 158-9). Schäfer admits the possibility that the visual area does extend beyond the limits of the occipital lobe and asserts that the cortex undoubtedly extends somewhat anteriorly beyond what is regarded the limits of the occipital lobe, especially on the under surface (and perhaps also the mesial surface).

The conclusions of Munk, Goltz and Hitzig, which were drawn from observation of dogs deprived of parts of the cerebrum, can not be applied directly to man, whose brain it has been the object to understand by the experiments upon animals. On the other hand, the results of Ferrier and of Schäfer are almost directly applicable to the brain of man, but in addition to the experimental results on animals there are numerous clinical observations on man of the visual and other sensory conditions following destruction of parts of the brain, and the results of these observations are of primary importance. Chief among the results that have been reported are those of Henschen (27, 28). This author examined all the available accounts of reported cases of blindness following lesions of the brain, and contributed observations of personal cases. From the consideration of the clinical accounts and of the pathologico-anatomical examinations he concludes that the visual center is limited to the cortex of the calcarine fissure, and that the centers for light and color coincide. He furthermore defined an area, in the anterior part of the calcarine fissure, to which he assigned a connection with the macula lutea, and disputed the conclusions of others who located the macular center in the cuneus. Regarding the lateral surface of the occipital lobes and the cortex of the angular gyrus, he says "I have not found documents which prove there exists a projection in this part, and a lesion of this part does not cause blindness" (28). This part of the cortex is, however, admitted by him to have something to do with vision and this fact leads to the conclusion that there are two areas: one restricted, in which there is a "projection of impressions," while the other, extracalcarine area, does not receive the impulses directly, and is more extensive. The calcarine area is conceived to be a sort of brain retina while the extra-calcarine area is supposed to have perceptive functions.

Vialet (73) using similar material concluded that the visual center extended beyond the calcarine fissure, including the cuneus, the lingual and the fusiform lobules, and part of the occipital pole. He concluded that lesions of these parts separately may be accompanied by hemianopsia, but Henschen has analyzed the cases of Vialet and has assured himself that the results obtained by the latter are in harmony with his own hypothesis. Against the hypothesis of Henschen, von Monakow has brought forth the fact that in cases of early blindness with total destruction of the optic nerve, where we expect to find the cortex wasted in the corresponding brain areas, the principal atrophy is to be observed over the convexity of the occipital lobes as well as along the calcarine fissure. The conclusion of von Monakow has recently been supported by Wehrli (77) who has examined histologically the brains in cases of blindness. He supports the view that the fibers from the macula lutea spread over a wide area at the occipital pole, and that the visual area is widely distributed and not to be limited to the area surrounding the calcarine fissure, not even to the part of the cortex with the cell lamination known as the calcarine type. He claims, furthermore, that purely cortical lesions causing hemianopsia have never been observed.

There are many cases reported clinically which seem to indicate that the localization of visual processes is not as limited as Henschen believes, but it must be said that the observations have often been poorly made, not only clinically but also pathologically, and it is difficult to estimate the value of the individual contributions. Of the negative results with the experimental method, the work of Vitzou (74-76) is of interest. He extirpated parts of the occipital lobes and of the angular gyri and found the animals lost their visual ability immediately after the operation, but recovered it to a great extent during the time they lived. In one animal he extirpated the occipital lobes but preserved the angular gyri. Although this animal was blind after the operation, this condition ameliorated in a month and a half, and after twenty-one months the animal was able to recognize its cage and people. A second monkey, in which both angular gyri and both occipitals were extirpated, was completely blind for about two months but following this period it began to recognize objects and persons. In a

third monkey, both occipitals and parts of both angular gyri were extirpated. This operation resulted in complete blindness for about two months, but at the time the report was made, about one year and three quarters after the operation, the monkey recognized objects and people. This animal is reported to have been able to see better than either of the two previously described animals. In a fourth monkey both occipitals and the posterior parts of both angular gyri were removed, causing complete blindness, which was much improved at the time of the report, twenty-one months after the operation.

Somewhat similar negative results have been reported by Panici (58) from the laboratory of Luciani. The conditions of three monkeys are reported, in which various operations were performed. In one animal the decortication of the posterior segment of the right calcarine fissure produced a bilateral homonymous psychical hemianopsia which persisted for only two days. In a second monkey Panici first extirpated the posterior part of the left cuneus. This resulted in no defect of vision, but following a second operation, in which additional cortex of the left occipital lobe was extirpated, there was found a condition similar to that in monkey 1, but which lasted only three days. Seven days after the second operation, Panici extirpated the whole left occipital lobe, and found a bilateral homonymous psychical blindness for about a month, which condition gave place to an amblyopia. A month later he extirpated the whole of the right occipital lobe, and found this to result in a right psychical hemianopsia for about a month, after which time the animal began to react to food, but remained indifferent to gestures and to a mirror, but with a corresponding amblyopia. At the first operation on a third monkey the internal portions of the right and left cuneate lobes were extirpated, and a week later this was followed by a more extensive extirpation. Neither of these operations appeared to have any effect upon the visual ability of the animal, but after the third operation, three weeks after the second, the complete excision of the left occipital was accompanied by a bilateral homonymous psychical hemianopsia, which continued for about a year. Twelve days after this operation the right occipital lobe was completely severed, which produced a complete

psychical blindness for one year. Thirteen months later a final operation on the left produced complete blindness in the right visual field, and three and a half months subsequent to the operation on the left the right hemisphere was destroyed up to the fissure of Rolando. After the extensive destruction just noted the animal became blind in both eyes, over the whole field.

These results of Panici are of very great interest for they show how much of the brain must be destroyed to produce a complete blindness, and also because they show how transient some of the visual defects may be. It will be seen in the experimental part of this article how closely some of the results of Panici resemble those observed by me.

By the method of recording electromotor changes in the brain, Danielewski (12) and Gotch and Horsley (26) found the occipital lobes responded to stimulation of the retina and the optic nerve.

After considering the various facts Schäfer (66) has summed up regarding the occipital lobes in man as follows: "There is abundant clinical evidence to show: That lesions of the occipital lobe produce disturbances of vision which are invariably of a hemiopic character. That lesions of the mesial surface of the lobe in the immediate neighborhood of the calcarine fissure are those which for their size produce the most serious visual disturbances. On the other hand, lesions of parts near to but not involving these parts of the occipital lobe have not infrequently been associated with defective appreciation of visual objects and particularly with word blindness. Perimetric observations in man show that in cases of hemiopia, produced by lesions of the cortex (of one hemisphere), the line of demarcation between the blind and functional parts of the retina usually passes, not through the middle of the fovea, but on the homonymous side, in other words, the fovea is not involved in the hemiopic condition." These, and the observations of animals following experimental lesions have led him to the following conclusions: "The whole of the visual area of one hemisphere is connected with the corresponding lateral half of both retinae. The upper zone of the visual area of one hemisphere is connected with the upper zone of the corresponding lateral half of both retinae. The lower

zone of the visual area of one hemisphere is connected with the lower zone of the corresponding lateral half of both retinae. The intermediate zone of the visual area is connected with the middle zone of the corresponding lateral half of both retinae. The focal point of the visual area, which is placed on the anterior part of the mesial surface of the occipital lobe, is connected with rather more than the corresponding half of the macula lutea of each retinae." With these conclusions von Monakow (47) is not in complete accord, although he considers the visual areas to be rather widely spread, and not be located in a small area.⁸ He believes the visual area for sensations extends beyond the calcarine area, and includes the lateral part of the occipital lobes, the cuneus, the lingual lobule and the gyrus descendens. More than this, von Monakow admits that the subcortical parts may have something to do with visual sensations (as mental phenomena), and if this be so, it would explain many of the apparently discordant observations and conclusions of experimenters and clinicians.

Throughout the previous discussion the psychological conclusions regarding the experiments upon animals and the observations of man have been reported as if they were of about the same character. This is not so, for we find the results have been interpreted to mean that the occipital lobes are the sensory receiving stations, or, on the other hand, that these portions of the brain are the places in which the visual associations (physiological and psychological) take place. From the first point of view the visual disturbances are considered to be inability to see, from the second they are conceived to be inability to perceive. This is the main point of difference between the adherents of Goltz and those of Munk. With the methods used by these investigators a solution of the problem is not possible, and the results which have been reported to us may be interpreted in either way.

Perceptions, etc. Regarding the psychic or higher intellectual functions of the occipital lobes little need be said. In an area close to the occipitals some have located the visual speech func-

⁸ "Diese und andere Beobachtungen hatten mich zu der Annahme geführt, dass die Stelle des deutlichsten Sehens überhaupt nicht in einer engen corticalen Zone repräsentiert sein könne."

tion, but others have placed this same function in the angular gyrus, to which it will be remembered Ferrier assigned such important visual functions. Optical agnosia, alexia and agraphia have all been located in the occipital lobes, but usually the location has been so indefinite that the individual localizations can not be discussed here. It may, however, be said that the more definite localizations are localizations in areas of the cortex and of the underlying white matter which can not be considered part of the visuo-sensory or of the visuo-psychic types of cortex. An examination of the diagrams of von Monakow and of Moutier in comparison with the cortical differentiation of Brodmann, of Campbell, of Bolton and of Elliott Smith will make this clear.]

EXPERIMENTAL.

INTRODUCTION

On account of the lack of information in regard to the functions of the areas (visuo-psychic) believed by histologists to be closely connected with the visual center (calcarine area), it appeared advisable to attempt to determine the functions of this so-called psychic area, and it was this problem which originated the present work. Subsequent developments directed the inquiry into other channels, and eventually it became imperative to reinvestigate the whole occipital lobe. Only part of the work has been finished but sufficient has been accomplished to indicate that the histological differentiation has not the physiological import which the histologists impute to it. The present work deals mainly with the relations of the lateral aspect of the occipital lobes in the monkey to certain sensory and perceptual states.

In this work eight monkeys were used, each of which was trained in visual discrimination previous to the extirpation or the destruction of parts of the occipital cortex. These animals were purchased from a New York dealer, and, as far as could be ascertained, had not been used for experimental purposes or for pets before the time of purchase. All the animals were reported to be about six to nine months old at the time they were received, although in size there was a considerable variation. During the nine months following their purchase they were utilized by Dr. W. T. Shepherd in psychological investigation, and after that period they were entirely in my charge. During the time they were under my observation they were fed mainly by me, but at other times by three other people. The animals were, therefore, well acquainted with the experimenter and they acted in as normal a manner as could be expected from animals kept in captivity. The observations of the animals continued for about fifteen months, at the end of which time all had been operated upon and killed. The animals lived, therefore, approximately two years, during which time they were under almost constant observation,

although the experiments to be reported in the present paper were not being conducted throughout all this period.

Two of the animals upon which operations were performed were shown at meetings of scientific associations, monkey 7 at the meeting of experimental psychologists in April, 1910, and monkey 1 at a meeting of the Georgetown University Clinical Society in February, 1910.

During the time the animals were under my observation they were kept in pairs or by threes in cages, 114 cm. high, 90 cm. wide, and 58 cm. deep. The front and right hand ends of the cages were covered with chicken wire, of one and one-half inch mesh. The top, the bottom, the back and the left side were boarded. Within the cage there was a shelf 30 cm. wide jutting from the back of the cage at a height of about 45 cm. This shelf extended the width of the cage. From the front of this shelf to the floor of the cage was a sliding door. When an experiment was to be conducted one of the animals (the one not working) was induced to get below the shelf, the sliding door was closed behind it and the monkey confined beneath, leaving the second animal free so that the experiments might be conducted without interruption and without disturbances.

The sliding door was kept open except at the time of the experiments, and the animals, which lived in these cages during the progress of the experiments, ran in and out of this space as they wished. There was, therefore, no cause for alarm on the part of the animal which was confined. The animals were not handled and the environment, except for the presence of the experimenter, was kept fairly constant throughout the day. Food and water, other than that used in the experiments, were pushed through or under the wire front of the cage and the animals took as much food as they wished.

Notwithstanding the animals were not handled, all became fairly tame, they would hang upon the wire netting of the cage and take fruit, nuts, bread, etc., directly into the mouth, and at no time did they appear to be disturbed by the presence of the experimenter.

In the accounts of the work which will be found in the section dealing with the observations of the animals before and after the

operations, it will be found that there are many expressions similar to those used in describing the actions of man. It must not be understood, however, that these expressions are used in the same way they are used for man, but solely for convenience and for brevity. It would, perhaps, have been advisable to describe the actions of the animals, but such descriptions to be intelligible must be accompanied by equally minute descriptions of the situations, and from the visual side can best or accurately be shown only by means of motion pictures. It must be understood, however, that the anthropomorphic method of describing animal activity is not to be taken as an indication that the animal had the same sort of mental process which a man would have under similar circumstances, but even the most careful of the animal psychologists have found it impossible to dispense with terms descriptive or indicative of mental processes in man. It would, for example, have been better to say "the animal turned its head and its eyes in different directions" rather than "the animal peered around the cage" but, on the other hand, with the warning that has been given, no one should interpret the animal activity in a way other than in terms of movement.

METHODS

Training. To one who is familiar with the studies on the functions of the cerebrum, it is evident that many of the differences in opinions and in conclusions have been due to the fact that the tests of animals upon which experiments have been made have been of such a character that they permit of more than one interpretation. It is certain that simple observation of animals following extirpation of parts of the cortex or following the injury to other parts of the nervous system is an inadequate method. For the reason that both the description of results of previous physiological work on the association areas were lacking in exactness and definiteness, about ten years ago, the writer (16-20) devised a method to determine more accurately the sensory and associative functions of parts of the nervous system, especially of the cerebrum. The first investigation to be performed by this method was one on the association functions of the frontal lobes (16, 17), but the method has been applied to

sensory functions both in the present work and in work published by others. This method has previously been described in various places and at present it may be said that it depends upon the formation of definite associations in an animal and the determination of the presence or absence of the associations after lesions of the nervous system. It will be readily appreciated that by this method there is an approach to the method the clinicians use in the examination of their human cases, and there is afforded the possibility of obtaining very exact information regarding the sensory or associative processes of animals even though in animal experimentation we are hampered, as compared with the investigations on man, by the lack of the definite means of communication by speech.⁹

Before an animal is operated upon we must become acquainted with its mental character, we must know the animal well before we operate so that we shall be better able to notice deviations from its normal mental character, following, let us say, the loss or the destruction of a certain amount of a certain part of the brain or the spinal cord. Usually it is not possible to keep a laboratory animal for a period of months or years in order to

⁹This method was used to a limited extent by a number of investigators before it was applied by me to the investigation of the frontal lobes, but all who had previously used it had employed it in much the same way as they made their regular observations. From the account given by Kalischer (36) of an investigation of the functions of the temporal lobes by this method, it might appear to one unacquainted with the situation that he were the originator of it. He calls it "meine Dressurmethode." To an impartial observer it appears a mere hair splitting matter to differentiate Kalischer's method of testing hearing in dogs from that of Thorndike (71), but throughout all of Kalischer's work there is evidence of total ignorance of the work which has been performed in America on animal psychology. It is of interest to note that following a critical note by me (20) Kalischer (37) relinquishes claim to the method as a whole, but makes a claim that he has used the most simple movement as an indication of the presence of sensation in the animal. This claim, in the way it is made, I am sure no comparative psychologist will admit, for the movement of the paw, or the movement of walking, is just as simple physiologically as the movement which Kalischer has used, viz., that of the snapping up of food, which must have associated with it other movements of the head. It is also of interest to note that Kalischer admits in his second article (37) some acquaintance with the training method that had been used by others (e. g., Gaule, 21), although no mention is made of this in his first article.

→ get acquainted with its mental make-up, and to facilitate matters we have at our command the training method devised by Lloyd Morgan and so ably followed out by Thorndike (71) and many others. By the use of this method we may have animals, which are to be operated upon, form certain associations, the presence or absence of which can be later determined by the experimenter in a few minutes. The associations always involve two elements, the sensory or afferent, and the motor or efferent. It is believed that in most, if not all, cases a third element is present, viz., the associational. By proper combinations and by the formation of more than one habit at a time it is possible to differentiate these three elements, and to infer without question which of the elements is lacking and which has been interfered with.

Comparative psychologists have investigated the visual discrimination ability of monkeys, but some have not been satisfied from the results and the methods of the experiments that monkeys discriminate colors as such. The methods of other investigators and the results obtained by them indicate that monkeys have good visual discrimination, although a few are unwilling to admit the conclusiveness of the experiments on color. It seemed advisable to have the animals acquire a habit indicative of color discrimination but none of the methods previously employed appeared to be sufficiently well accepted and none appeared to place the animal in a position similar to that it might normally be in. In the present work an attempt was made to have the animal tested in as normal a way as possible, and to form the habit or to produce the discrimination quickly as well as naturally.

In the present work it was necessary to have the animals form habits of a definite visuo-motor character. For this reason the sensory part was made as simple as possible, viz., foods of different colors, which had to be discriminated. In a series of experiments on the color discrimination of monkeys, conducted by Dr. W. T. Shepherd (68), under my direction it was found that the animal rapidly learned to discriminate colored objects if the stimuli were of a character to attract and to hold the attention. In most animal experimentation it has been found difficult to get stimuli which will attract the attention of the animal, stimuli which are appreciated by the animal and which will lead

to definite reactions. In color experiments it has been customary to use the box method of feeding, the box being covered with colored paper or lights being exposed near the box. The employment of this method has certain advantages and certain disadvantages that are apparent to all who have used it. On the one hand the colors may be changed to a considerable degree both in intensity and in hue, but on the other hand the use of papers, filters, or other similar means of giving stimuli introduces an element foreign to the animal mind and must have less effect than the exhibition of colors in direct connection with the object to be obtained. Moreover, in order to determine discrimination ability many investigators have found it necessary to punish the animal for a wrong selection and to reward it by means of food for a correct selection. In most of the work which has been reported the punishment has also been something foreign to the animal mind, and the use of electric shocks and other similar methods to inhibit the activities of an animal have led at times to disturbances in activity which are not conducive to proper experimentation.

Because of the difficulties and disadvantages of the methods which have been previously employed, colored food was used in the experiments of Dr. Shepherd, and in these experiments it could not be doubted that the attention of the animal was directed toward the stimuli. In the early work bread or rice was mixed with appropriate colors, two or more differently colored pieces of food were simultaneously displayed before the animal and the animal learned to select one or more of the colored pieces. The artificial method of punishment was discarded in these experiments and a more natural method was employed. In the method the punishment and the cause of the inhibition of the wrong reactions were contained in the stimuli and were not extraneous. Certain of the colored foods were soaked with a solution of quinine and others had added to them a certain amount of saccharine. On the assumption that the monkey likes sweet and dislikes bitter tasting foods, we should find that the animal would learn to decline the bitter food and to take only those which were sweet or at least not bitter. As a matter of fact, this assumption was found to hold in almost all the animals tested. With only one

monkey was there any difficulty in the establishment of the habit to take the properly colored and sweetened food and to leave the food which had been made bitter. This animal seemed to have little objection to the bitter taste and for a relatively long time ate both the sweet and the bitter foods. This animal died before the effects of the operation were determined and the records are not included in the accounts of the experimental work. Eight other monkeys, however, had a decided dislike for bitter food, or to express this in terms of reaction, these animals soon learned to permit the bitter foods to remain on the plate, and although hungry, did not touch them. In the formation of the habit and in the subsequent tests following the operation the monkeys were not kept in a state of absolute hunger, for it was found by previous work that this factor would interfere with the normal working of a monkey.

In performing the experiments to be described here the animal was in its usual cage. The cage has already been described. The animal sat upon the shelf, sometimes near the wire netting on the right hand side and sometimes farthest away from the netting. A glass plate, 12.5 by 18 cm., was arranged on a platform with cup hooks to catch the wire of the cage so that it could be at-

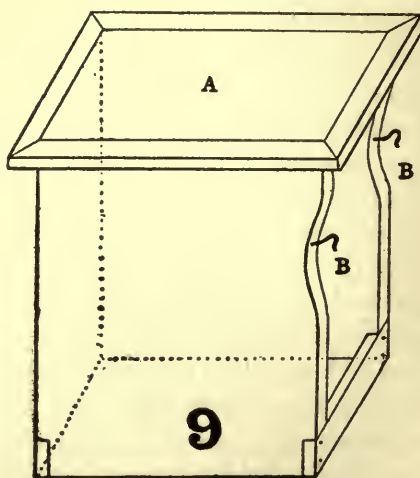


FIG. 9. Glass plate and holder for the presentation of food to the monkeys. A, glass plate; B-B, cup hooks to catch upon the wire netting of the cage.

tached to any part of the front or side of the cage. The arrangement was such that the glass plate was kept horizontal. Fig. 9 illustrates the glass plate and the holder. All this part of the apparatus was colored black. The food was placed upon the glass plate, the holder was arranged on the cage and the experimenter moved away from the cage about a meter's distance. The animal, which usually sat at the farthest end of the platform, moved forwards and took the food which was presented to it on the plate. In performing the experiment in this manner the greatest possible freedom was accorded the animal, and the movement to be performed was as simple as possible and one which would give the right to conclude that discrimination did or did not take place, i. e., the taking or leaving of the food. The arrangements at a later date were made more simple, as far as the adjustments are concerned, in that the glass plate holder was attached to the cage at the beginning of the series of tests and kept there throughout the series on that day. When this was done the food was placed upon the plate in the same manner as has been described. In all the series of tests the arrangements of the breads were constantly changed, the bitter being at times on the right, at times on the left, and if three or four pieces were simultaneously displayed the bitter pieces were between the sweet, or at both ends. In most of the experiments, all of those in which the animal was being trained, the two or more pieces of food were placed upon the plate at approximately the same distance from the cage netting. In later tests at times the foods were arranged indiscriminately on the plate, the sweet being farther from or nearer the cage, etc. Most of the animals were trained on the discrimination of colored foods, and one on the discrimination of foods of different sizes.

The colored food. After a number of tests it was found that white bread was most suitable both for coloring and for food. The bread was usually 24 to 48 hours old at the time it was received. The crust was removed and the bread was cut into thin slices about 5 mm. thick, then into strips of about the same width, and finally into shorter lengths making hexahedrons, approximately cubes, 5 mm. on each edge. A large number of these were cut at one time and from 30 to 100, depending upon

the number of animals under the test, were colored; the remainder were used on succeeding days. If kept uncovered the small cubes dried, but it was found that the immersion into the solutions brought them back to their original size. The cubes were dipped into watery solutions of different colors, and thoroughly saturated. The resultant colors were fairly homonymous, but did not have the smoothness of colored papers or of other similar material on account of the small bubble holes in the bread. The colored moist breads were placed in small crystallizing dishes and covered with watch glasses to prevent the entrance of dust and to limit evaporation. In this way it was found possible to make up fairly large quantities of the different colors and to keep them fresh and moist for several days.

In the general experiments on color four differently colored breads were prepared: red, blue, green, and yellow. The color solutions, formulae for which follow, were made up in large quantities, and to each solution a proportionate quantity of alcoholic solution (5%) of thymol was added. The thymol was added for two reasons; first to prevent the formation of mold in the solution and, secondly, to overcome any special odor of the solution and to substitute for the special odor that of thymol. In this way an attempt was made to equalize the odors of all the stimuli, in order that the discrimination might not take place because of the differences in odor. Particular attention is called to this factor, for although we have no right to say that by this introduction of a foreign odor (distinctly perceptible to man) the odors of all the pieces of bread were the same, I believe the strength of the solution was sufficient to overcome any odor of the individual solutions. None of the individuals (men) who were tested could detect the least difference in the odors of the solutions, and the tentative conclusion was drawn that the individual odors of the solutions were overcome, and that all the breads smelled alike.

The formulae used in making the solutions were as follows:

Red: Congo red.....	1.0 gram.
Water	300.0 cc.
Saccharine	3.0 grams.

Blue: Toluidin blue	0.5 gram.
Water	400.0 cc.
Saccharine	4.0 grams.
Yellow: Methyl orange	0.5 gram.
Water	250.0 cc.
Quinine bisulphate (0.5% solution).....	25.0 cc.
Green: Methyl orange	0.2 gram.
Smaragd grün	0.1 gram.
Water	250.0 cc.
Quinine bisulphate (0.5% solution).....	25.0 cc.

When they were intended for use, i. e., for the dipping of the bread, the solutions were diluted to one-half strength by the addition of water.

Immediately after dipping the breads the colors of the breads were compared with the colored papers in the Milton-Bradley series. On this comparison it was found that the yellow bread was approximately half-way between the yellow orange and the orange yellow of that scale, but after slightly drying the color was more nearly like the latter.¹⁰ The red bread was approximately like the red of the scale, although on account of the chemical properties of the Congo red this color varied to a greater extent than did any of the others. When the bread was dipped into the blue solution it took a color most like that of the Engine colored paper 5b of the scale, being close to the regular blue shades nos. 1 and 2. When the solution was diluted to half strength, as usual, the bread became nearly like Engine colored paper 5, or like the blue of the regular scale, although the latter was a trifle darker. The bread, after having been dipped into the green solution almost exactly matched green yellow shade 1, but on standing this color changed to yellow green shade 2, and eventually became almost like yellow green. The change in this case was probably due to some combination with the air, probably oxidation.

No special examination of the colored solutions by means of

¹⁰ The colors of the breads are given in terms of the nearest color in the Milton-Bradley scale, but the comparison is rough, and in the case of green 2, the color scale showed nothing to correspond closely. The color of green 2 was much darker than the M-B green shade no. 2, but there is nothing in that scale to give a better idea of the color and shade. The difference in the colors, is, however, the main fact to be remembered.

the spectroscope or by the photometer was made, because all the colors are standard colors, and can readily be made by anyone, and because this examination was not deemed of importance in the present work.

Color Vision of the Monkey. It has been said above that the animals soon learned to discriminate the colored breads, leaving the bitter ones and taking the sweet. At first this may be taken as sufficient evidence that the discrimination was made on the basis of the color quality, but to this conclusion many animal psychologists will take exception. On account of the doubt on this point a supplementary series of tests were made with several monkeys to determine whether the hue or the difference in intensity (or brightness) was the factor which was discriminated. The tests of one animal will suffice to make this matter clear.

With this animal breads colored red and green were employed. After the animal had learned to discriminate the two kinds of bread, the colors were changed in intensity or in saturation and additional tests were then made. In the original tests (before the changes in the intensity, etc., of the colors) in making up different lots of colored breads the pieces showed slight differences in intensity and in saturation, and to a greater extent in moisture. These variations were not of sufficient amount to be particularly noticeable by me or by others, and were determined only when the breads colored at different times were placed side by side and examined in very bright light. There was also a very slight difference in the colors of the individual pieces of bread, but under the most favorable conditions these differences could not be detected at a distance of about a meter. In performing the experiments the colors were placed on the plate simultaneously but in an irregular position; half of the time the red was to the right of the animal and half to the left. Sometimes the red and sometimes the green was nearer the animal. In this way no association could be formed between positions and the tastes.

Experiments in color (beyond these performed by Dr. Shepherd, to whose work reference has been made) began with monkey 6 on November 30. On that day in the first test the animal took both pieces of bread, red and green, and immediately placed them in her mouth and ate them. She did not appear to enjoy the

taste of one of the pieces and became more cautious after two trials, and on the third trial she partly rejected the green (bitter). On seven other trials on this day the animal took only the red bread (sweet). On the following day she took only the red. Three days later she took both the red and the green in the first seven trials, and only the red the other three trials. A rest of two days was given, and, following this, on twelve successive days, ten trials each day, there were only three mistakes. At the end of this time it was concluded the habit was firmly established. The animal would not take the green bread, no matter what position it occupied on the plate. At times the red bread was placed as far away as possible, and at other times to the extreme right or to the extreme left while the green was in the most prominent place, viz., the center of the glass.

On the following day the conditions of the experiment were altered. Instead of presenting to the animal only the definite colors with which it had become familiar and to which it had learned to react in a definite way, marked variations of these colors were presented. Each of the stock solutions for this experiment was mixed with different quantities of water, and in this way there was obtained solutions giving (to man) four distinct shades of red and four of green. The mixtures which gave the different colors and the color results on the bread (according to the Milton-Bradley scale) of saturating the bread with these mixtures are as follows:

Red 1—(red, shade no. 2) 16 cc. standard red solution, 40 cc. water, and a piece of sodium carbonate the size of the head of a pin.¹¹

Red 2—(red) 16 cc. standard red solution, 40 cc. water, and sodium carbonate until the solution began to clear.

Red 3—(orange red) 16 cc. standard red solution, 40 cc. water, and sodium carbonate until the solution became clear.

Red 4—(red, tint no. 2) 10 cc. standard red solution, 50 cc. water, and sodium carbonate until the solution became clear.

Green 1—(yellow green, shade no. 2) 20 cc. standard green solution and 50 cc. water.

¹¹ The Congo red is an indicator for acids and alkalies, and the color of the solution depends upon the relative amounts of these opposing conditions. The color of the solution was readily altered by the addition of small quantities of sodium carbonate and the greater or less quantity of this alkali gave the various shades and tints of the red.

Green 2—(green, shade no. 2) 35 cc. standard green solution, and 20 cc. water.

Green 3—(green, tint no. 1) 15 cc. standard green solution, and 25 cc. water.

Green 4—(yellow green, tint no. 1) 10 cc. standard green solution and 50 cc. water.

Two of these colored pieces of bread were presented to the monkey in the same manner as the breads to which it had learned to react. The breads were selected and arranged in an irregular order; red 1 and green 1; red 1 and green 2; red 2 and green 1; red 3 and green 3, etc. With these combinations twenty tests were made and in every test the animal took the red bread and disregarded the green. Twenty tests on each of two succeeding days gave the same result; green of any shade or tint was not taken, the red bread of any shade or tint was taken. Three days later twenty-two tests with two of the colors gave almost the same result, and two tests in which two pieces of green and two pieces of red were presented simultaneously showed that the animal would take the red and disregard the green even when the conditions of the test were changed in this particular. Following is a record for this day:

December 23, 1909. Monkey 6, reactions to shades and tints of red and green. R1, R2, R3, R4, G1, G2, G3, G4, are the different shades and tints used. The color noted first in each test was placed at the left of the plate.

- | | | |
|------------|-------------|---------------------|
| 1. R1, G1. | 9. G4, R1. | 17. G3, R3. |
| 2. R2, G2. | 10. G4, R2. | 18. R4, G3. |
| 3. R3, G3. | 11. G2, R1. | 19. G4, R1. |
| 4. R4, G4. | 12. G2, R2. | 20. R2, G4. |
| 5. R1, G4. | 13. R3, G2. | 21. R3, G4. |
| 6. G4, R4. | 14. R4, G2. | 22. R4, G4. |
| 7. R2, G4. | 15. R1, G3. | 23. R1, G1, G4, R4. |
| 8. G4, R3. | 16. G3, R2. | 24. R2, G2, R3, G3. |

In test 4 the monkey took the red piece first and after it the green; in all other tests only red was taken. Eighteen days later the monkey made no mistakes in 13 trials with two pieces presented simultaneously. Following is the order of the tests:

- | | | |
|------------|-------------|-------------|
| 1. R1, G2. | 6. G4, R3. | 11. G1, R4. |
| 2. G2, R3. | 7. G4, R2. | 12. R2, G1. |
| 3. G2, R2. | 8. R4, G4. | 13. R4, G3. |
| 4. R4, G2. | 9. R1, G1. | |
| 5. R1, G4. | 10. G1, R3. | |

Another monkey which was tested picked out the shades and tints of red when the number presented simultaneously was more than four, and two other animals made no mistakes on the different shades at a later date although the colors were not so defined as they were in these experiments. Even when other colored solutions were used for the dipping of the bread the animal always selected the red in preference to the green. In some of the later tests the red bread was made by dipping the pieces into Carter's crimson ink, and the green by dipping pieces into a mixture of blue and yellow drawing inks (Columbia brand). These later tests were made also without having the solution mixed with thymol solution, and without the addition of saccharine and quinine. It appears from these tests, therefore, that neither the smell of the thymol nor the presence of the saccharine affected the reaction after the habit was established and that the reaction was one due to the color of the breads.

In further tests with monkey 6 in which some of the colored pieces of bread were of a larger size, 10 to 12 mm. on each edge, and some were of the smaller usual size, the combinations of the small with the large did not affect the reaction to the color. The following combinations were made: A, small red with a large green; B, small red with small green; C, large red with large green; D, large red with small green; tints and shades varying as has been described. In these tests the red was selected regardless of size, tint or shade; the green was always disregarded.

The results of these experiments indicate plainly that the monkey which has been taught to react to a particular situation is able in some way to transfer this practice to a situation, which has certain elements of similarity, or, to put the matter in more definite terms, the monkey which has learned to react to definite colored objects in some manner extends this mode of reaction to shades and tints of the same hues. Two explanations may be offered for this result; that the animal has in each case reacted to the hue of the object or that it has reacted to some other factor. The experiments with the different sizes shows that the reaction was not to size. The fact that the colored breads were placed on the plate in irregular order indicated that the reaction was not due to the position. Because the animal disregarded the differ-

ence in intensity of the colors and continued to react in an appropriate manner regardless of the intensity differences is an indication that the intensity relations of the breads was not the important factor, and because other reds and greens (with presumably different absorption spectra, although this was not determined) were selected by the monkey in the same manner, the indication appears plain that the reaction was due to the color or hue. From the tests, especially when we compare them with other tests on animals performed by others, it seems justified to conclude that monkeys do discriminate colors, and that in the present work the discrimination was one of color and not of other elements in the stimuli.

Operation. Each monkey was caught in a bag and anesthetized in it before being prepared for the operation. This was found to be necessary on account of the struggles of the animal from the anesthetic and binding, and after the anesthetic was begun it was continued throughout the time the operation was in progress. As an anesthetic I used the A. C. E. mixture. This I found was well taken by the animals, it decreased the time of excitement, and was much safer than when chloroform alone was given. The recovery was rapid and attended by no adverse conditions.

After having been anesthetized the animal was placed upon an operating board, and tied thereto. The hair over the head and over the back of the neck was cut closely, and over the part where the incision was to be made a depilatory solution or paste was applied. This was found, as in my previous work, to be an excellent method of removing the hair, and was much easier than the method of shaving. In shaving it has been found that the skin is sometimes broken and this introduces an extra wound which must be attended to or the chance of infection is increased. Moreover the depilatory produced a "close shave" removing the fine hairs as well as the coarse ones. The mixture employed by me was made by combining equal parts of precipitated chalk and barium sulphide, and adding sufficient sterile water to make a paste.¹² This was applied to the head, as has been mentioned and

¹² I tried upon myself various mixtures, but found the most satisfactory results to be obtained with the mixture of chalk and sodium sulphide, calcium sulphide, and barium sulphide. The calcium and sodium sulphides did not work as rapidly as the barium, and were apparently more irritating, so that in all the experiments with the monkeys the barium sulphide was employed.

in from three to five minutes the hair was removed by scraping away the paste. The head was then washed with bichloride solution, 1 : 1000, and a gauze sponge soaked in the solution of bichloride was applied to the head, and left there until the operation was begun, i. e., about 3 to 5 minutes.

The instruments had been sterilized by boiling in a solution of sodium carbonate, and the dressings had been sterilized in a pressure steam sterilizer. After having carefully attended to the matter of sterilization, the operation was begun. The apparently great trouble taken for the production of asepsis was repaid by the results of the operations, in only one of which were signs of infection found, and this case was readily explained and will be mentioned below.

A median incision was made in the scalp and a second one was made at right angles to the original one, about at the place the skull openings were to be made. The skull was opened by the use of a half-inch trephine, and in most of the operations this opening was enlarged by bone forceps to three or four times the original size. In some of the operations the brain was incised with a fine cataract knife, for the purpose of separating the occipital lobe from the remainder of the brain, but in most of the operations the cortex was cauterized by means of a galvano-cautery. The depth of the burning varied in each case, in each hemisphere and even in different parts of the hemisphere, but these results will be mentioned in the appropriate experimental sections. The trephine buttons were seldom inserted. Bleeding from the diploe was checked by the application of bone wax, and the bleeding of the brain was usually controlled by the application of compresses wet with normal saline solution. At times it was necessary to apply a small quantity of Suprarenalin, 1 : 1000, which effectively checked the hemorrhage when it was used.

After the operative interference with the brain the dura was drawn over the brain, but was not sutured. The scalp wound was closed, and over the site of the scalp wound a layer of gauze slightly thicker over the site of the removal of the bone, was placed. A cotton bandage was then arranged around the head, to include the jaw, but leaving out the ears. After sufficient layers of this had been applied it was sewn with strong thread to

prevent its removal by the animal. The bandage was picked at by the animal but in no case in which the sewing was thoroughly performed did the monkey cause it to fall off. The constant picking frayed the edges and after a few weeks the bandage entirely disappeared from the head, and was found encircling the neck like a ruching. Long before this time, however, the wound had healed and the removal of the bandage did not affect the wound. After the bandage was removed it was usually found that the hair had begun to grow. With one animal the bandage was hurriedly sewed, on account of the rapid recovery from the anesthetic, and the whole bandage was found to have been removed within three hours after the operation. Even this animal did not show signs of infection at the autopsy. In this case a new bandage was applied after the head was thoroughly washed with bichloride solution.

Post Mortem Examinations. One animal was killed with illuminating gas, and the others were given overdoses of chloroform. In most cases the autopsy was performed immediately after death, and in only one was there a delay of as much as two hours. The brains were weighed as a whole, and no effort was made to separate the cerebrum from the cerebellum and pons, etc., nor to get the separate weights of the hemispheres. It was found inconvenient at times to get the brains weighed at the time of the autopsy, and those which were not weighed at the time of the autopsy were weighed after having been preserved in alcohol (95%) or in formalin (10%) for 24 hours.

Some of the brains were photographed immediately after the autopsy, but a few were photographed after having been in alcohol or in formalin. From the photographs tracings were made, showing all the principal points, fissures, etc., and the illustrations accompanying this article are reproductions of these tracings. Whenever a brain was photographed it was placed on a scale showing centimeter and half centimeter divisions, and these divisions are marked in the illustrations. The surface diagrams are, therefore, approximately accurate representations, and on account of the presence of the scale the accurate sizes of the brains may be determined. The illustrations are reductions from the tracings, in some cases to one-half size, in others to two-thirds

size of the originals. When the hemispheres were cut for the purpose of rapid hardening and impregnation, sketches were made of the appearance of each section, with the apparently abnormal parts distinctly marked.

After complete hardening, sectioning, staining and mounting of the sections they were placed in the Edinger projection and drawing apparatus and accurate sketches made of all appearances. The magnification was usually about three to four diameters. On each of these drawings the scale was drawn. Reductions of these sketches are reproduced.

The sections were examined microscopically by Dr. G. R. Lafora, and the results of his examination are noted on the diagrams. Wherever the cortex or pia or fibers were diseased marks were made on the drawings (Edinger) and at the same time Dr. Lafora marked the limits of the so-called visual (i. e., calcarine type) cortex if these were determinable. At times it was found that all distinctive marks of the calcarine cortex had disappeared from the lateral aspect of the hemispheres, and at times it was even difficult to note the limits along the calcarine fissure. In estimating the amount of destruction and in drawing this on the diagrams it was done conservatively, but on the other hand, on account of the negative character of some of the results, there was a liberality in defining the limits of the calcarine cortex. It is possible that other observers would have judged these two limits to be closer together than they are pictured in the accompanying illustrations.

Following is a summary of the histopathological findings by Dr. Lafora: "The lesions of the pia may be summarized as follows: In places where the galvano-cautery acted directly upon the pia (i. e., burned it) the pia was found to be completely destroyed. In certain cases and in certain places the following effects of partial destruction were found: hemorrhagic processes with an accumulation of polymorphonuclear leucocytes and Körnchenzellen (full of pigment and fat) and a hyperplasia of the fibroblasts. These are reactive processes consequent to a partial destruction or to an irritation of the pia a short time previous to the examination. A similar condition, though not so marked, is found in the pia over a comparatively large area sur-

rounding the cauterized regions, but the pial alterations in the latter cases are not accompanied by cortical changes as are those in the cauterized area. In the cerebral cortex numerous pathological changes, especially different forms of degeneration, have been found. When the pia was totally destroyed the cortex was found to have disappeared, and to be replaced by an accumulation of blood cells with polymorphonuclear leucocytes, around which there were many Körnchenzellen and macrophages. Around the necrotic zone, which sometimes extended to a considerable depth into the white substance, was another zone of a reactive character. In this secondary zone there were found marked hyperplasia of the blood vessels, many fibroblasts showing a transformation into macrophages, and hyperplasia of the glia cells. The nuclei of the glia cells frequently showed karyorrhetic processes, and these cells were charged with pigment, and apparently took the functions of the Körnchenzellen. When the pia was only partially affected there was produced a marked reactive process, in which condition we found very different lesions. At times it was found that the zone agranularis was destroyed and the other cortical layers were only slightly affected by a neuroglia hyperplasia and many ganglion cells showed tigrolysis and neurophagia. At other times the process was more marked in the middle layers of the cortex (granularis interna and ganglionaris of Brodmann) while the zona agranularis (lamina zonalis of Brodmann) and the lamina pyramidalis were not much affected. These conditions are undoubtedly dependent upon the different vascular destructions. In the last described conditions in the vicinity of the cortex in which the lesion was pronounced there were always found indications of irritative changes (neurophagia, neuroglia hypertrophy and hyperplasia), the vessels showed many Körnchenzellen in the lymphatic spaces and there were also observed neuroglial Stäbchenzellen. We observed hemorrhagic, necrotic and reactive processes. Where hemorrhages were produced a reaction around these areas was always found. Sometimes the obstruction of a vessel produced a necrotic process in the depth of the white substance, with a preservation of the cortex. In the brains of the animal operated upon by cutting, the degenerated elements (fat formation) were not well marked on account of

the short time intervening between the operation and the time of the examination. In these cases, however, some fat spherules were found, as the drawings indicate."¹³

It may be said that the examinations of the brains were made after staining by the methods of Nissl and Marchi.

One point mentioned in Dr. Lafora's account of the lesions is worthy of special attention, viz., the fact that in certain places it was found that destruction of the pia was not accompanied by destruction of all of the underlying cortex. In selecting the cautery method of extirpation it was believed that the burning of the cortex with the consequent obliteration of the vessels would produce an anemia of the cortex, and a consequent destruction. By the use of injection methods Beevor (4) concluded that the cortex is supplied by the arteries passing through from the pia.¹⁴ The results of the histological examinations in these cases appear to indicate that not all parts of the cortex are supplied by the pial vessels, and that some parts of the underlying white substance may be supplied. Some of the more interesting, but finer observations on this point have not been mentioned in the account of Dr. Lafora, but it appears true that contrary to Beevor's view the cortex is not entirely supplied by the pial arteries. In some cases, as has been mentioned in the above account, there has been a selection even in the different layers of the cortex, and it is neither true that all the cortex is destroyed nor that it may be preserved entirely.

¹³ In all the figures (except 93 to 96) indicating the conditions found by microscopical examination, dots are made to indicate the location of hemorrhagic processes and crosses to indicate the destructions of pia, cortex, fibers, etc. In figs. 93 to 96, the degeneration of masses of fibers could not be well shown by crosses and the degenerated bundles are shown by dots and lines. The following abbreviations are used in the figures: *R*, right; *L*, left; *calc.* or *calc. fiss.*, calcarine fissure; *cent.*, central or Rolandic fissure; *Sylv.*, Sylvian fissure; *par.*, parallel fissure; *occ.*, occipital fissure; *thal.*, thalamus; *lent. nucl.*, lenticular nucleus; *vent.*, ventricle; *posterior* (in figs. 30-35) indicates the posterior portions of the sections; *c* indicates the limits of the calcarine type of cortex.

¹⁴ "I hold with Duret that the arteries which penetrate and supply the cortex are end arteries, and do not anastomose with their contiguous branches; and I have found that, if the pia matter be carefully removed, or a circular cut be made in it, the subadjacent cortex is not injected by the vessels in the surrounding cortex."

RESULTS

Eight monkeys were used as the subjects in this work. These, as has been said, had been previously used in an investigation on animal intelligence by Dr. W. T. Shepherd, and in the early work they were given numerical designations instead of names. These numbers were adhered to in the present work, although they do not conform with the order in which the observations or the operations were made. The following accounts of the experiments are, however, given in accordance with the serial numbers for the purpose of convenience.

An examination of the case records reveals a variety of operations, and a variety of observations on different aspects of monkey intelligence, some of which can, and some of which can not, be correlated with the brain conditions.

Monkey 1. This animal was trained to discriminate yellow (bitter) from red (sweet) bread. The experiments for the production of the habit were begun September 23, and continued over a period of more than two months before an operation was performed. In the training, tests were made on 29 days of the whole period. Following is an abbreviated account of the process of learning: Sept. 23, 10 tests; took yellow bread twice and the other eight trials left it, but always took the red bread. Sept. 24, 10 tests; similar result, except that the monkey did not place the yellow in its mouth the second time it picked it up. On the two succeeding days there was a similar result, although on the fourth day the animal more often picked up the yellow bread. On the two succeeding days the monkey always picked up and ate the yellow bread. On the two succeeding days the monkey always picked up and ate the yellow bread, and did this apparently from hunger, although he did not seem to like the taste. On Sept. 30, 10 tests; the animal first showed perfect discrimination, for it always took the red bread and left the yellow. Two days later a similar result was obtained, but on Oct. 4, after one day's rest, the animal once more took both the red and the yellow. From this time there was a gradual curve of learning, with only slight variations, to Oct. 19, after which time the monkey made very few mistakes. On November 3, the animal performed the ten tests satisfactorily, and a rest of fifteen days was given, at the end of

which time a "memory test" was made. This latter showed perfect retention. After five days another series was made, showing perfect retention, and again three days later, Nov. 27, with the same result.

Operation: November 27, 11 a. m. The occipital lobes were severed by a cut posterior to the parieto-occipital fissure. During the operation there was little loss of blood from the scalp, bone and brain, except on the right side where there was considerable hemorrhage when the incision was made into the brain substance. This part of the brain was compressed for about ten minutes, and at that time the blood flow ceased. The trephine buttons were inserted, the head was bandaged, and the animal was taken from the operating table at 11:30.

Immediately after the operation the eyes were widely dilated, and the animal appeared to be only semi-conscious.

Two and one-half hours later the animal was found sitting up in the cage in which it had been placed, but it was in a huddled attitude. When a lump of sugar was handed to it, it took the sugar but threw it upon the floor of the cage. It took a piece of cotton wool, which had been rolled into a swab, and threw it upon the floor of the cage. Its attention could be attracted easily when noises were made, and it started when touched and when the door of the cage was shaken. When the hand of the observer was placed near the cage netting the animal put one of its hands in that direction, and at times took hold of the finger. The movements that were made were slow and indecisive, and the errors made in putting its hands through the wire netting were from 2.5 to 5 cm., i. e., one to two meshes of the netting. When the gaze was attracted to an object held in the hand and a lump of sugar was exposed in the other hand of the observer, but peripherally to the fovea, the animal would sometimes turn to the sugar, but most, if not all the movements of attention appeared to be due to the sound stimuli rather than to visual sensations. In one visual respect the animal was quite unlike a normal animal; it kept its gaze fixed on one point for comparatively long periods, and the quick shifting gaze of the normal animal was entirely lacking. When no sound was made, and movements of the observer were at a minimum the animal remained absolutely quiet,

the eyes became staring, the eyelids gradually lowered, until the eyes were covered almost completely. Slight noises or movements (which very likely produced noises although they could not be seen) waked the animal immediately, and there was a return to the sleepy condition immediately when quiet again reigned. The pupils were medium in size.

Thirteen hours after the operation, the animal was looked at; when the light was turned on the animal came from behind the door of its cage, looked at the observer, and appeared to be bright. No special observations were made at this time.

Thirty-two hours after the operation, the animal was with some difficulty removed from its sleeping box to the observation cage. Sticks introduced into the sleeping box to persuade it to change its quarters were taken hold of and twisted away from its body. When it went into the observation box, it was presented with a lump of sugar, which it took with a rather awkward movement, and immediately placed in its mouth. Several times it took the sugar from its mouth, held it in its hand and looked at it, and returned it to its mouth again. When the end of a stick or the finger was put a short distance through the wire netting of the cage the animal made movements to take hold of these things. The movements were not the quick lightning-like movements that a normal monkey makes, but slowly executed and inaccurate. The arm moved toward the goal, or rather, in the direction of the goal, but when the hand of the animal was about 5 to 8 cm. away from the object an additional adjustment was made so that the finger or the stick could be grasped. It was apparent that the initial adjustment was very inaccurate, that the distance was not properly sensed, but that the discrepancy was appreciated, and that the secondary or later adjustment was considered necessary. The actions of the animal during these tests could be compared best to those of a child or even of an adult who tries to make a new or unaccustomed movement, of a rather complex character, and who attends to the movement with the eyes as a guide. ✓

The indefiniteness or impairment of the movement may have been due to one or more of several factors: (1) the loss of rather definite visual sensations which are normally present and ✓

important in the adjustment of movements; (2) to a motor disturbance; or (3) to a loss of kinesthetic sensations from the eye. That there was no motor disturbance was apparent from the movements of a reflex character made by the animal. The bandage was apparently disagreeable, and caused some irritation. At times the animal put its hand and plucked at the bandage near the ear, pulled at it and endeavored to get rid of the irritation. These movements were performed accurately, quickly, and without the second adjustment which was noted in the case of the movements of taking hold of the finger or of the stick.

The following day the animal gradually improved, and it was impossible for me to determine any visual defect. The movements continued to be a trifle uncertain, but this was all that was observed to be different from a normal monkey.

Two days after the operation the animal was tested with the colored breads. In these tests, the animal made no mistakes, although at first the animal was not as quick as normal, and it was usually necessary to wait a longer time for the animal to select the bread. In the tests there was no memory or association loss, and, as far as could be determined, the animal reacted to the colors just as it had done previous to the operation. After an interval of a day the animal was again tested and found to retain the ability to discriminate the colored breads, and from this time there was no appreciable disturbance in the behavior of the animal. This animal could, therefore, see, and there was neither a visual disturbance similar to the permanent blindness noted by many observers, nor to the temporary blindness recorded by Ferrier. Objects in all parts of the field were accurately seized and apparently discriminated, and no defect of the nature of restriction of the field of vision or of a segmental blindness was found.

Four months later a second operation was performed. In the intervening period the animal was not practiced much on the color discrimination, but sufficient tests were made with him so that this habit was not forgotten. No other visual discriminations were taught to the animal. During part of this time the discrimination tests on the red and yellow showed that

at times the animal took occasionally the yellow piece of bread, smelled it, or tasted it and sometimes even ate it. In a series of ten tests this was found to occur but once, and to be as often in the middle of a series as at the beginning. The animal was well fed during this period, and at times refused to work with the colored breads, so that only three to five tests were made on certain days. Following are accounts of the color tests immediately previous to the second operation:

March 29, 10 tests: in the second test the monkey took the yellow and the red at one time and placed both in the mouth and ate them; the tenth test the animal did not take either of the pieces, although I waited five minutes; in the other eight tests the animal took only the red bread and this was taken immediately and without hesitation. March 30: the first seven tests were made in the usual manner, the animal taking the red bread as soon as the breads were presented; in the eighth test the animal took the yellow with the left hand (in all other tests the animal had been taking the bread with the right hand) and tasted it, but threw it away without eating; the results of the ninth test were correct, but the monkey did not take the red bread on the tenth test until after thirty seconds. March 31, 5 tests: in the first test the animal took the yellow bread as well as the red, but threw it away after having tasted it; the other four tests were correct. April 1: on the first test the animal took the red bread and left the yellow, but did not take either piece on the second test and the tests had to be discontinued.

Second operation, April 1.—The trephine openings were made farther back in the skull so as to expose the tip of the occipitals. The buttons which had been inserted at the time of the first operation were found to be present, but softened and adherent to the dura. When they were taken away there was considerable bleeding. Both openings (including the two trephine openings on both sides) were enlarged with bone forceps. The dura was cut to expose the surface of the occipital areas. The cortex was then burned with the electric thermo-cautery at a red heat. The cautery was passed over the lateral aspect of the lobes,

and inserted into the mesial part. The operation was finished in an hour (12:30 p. m.).

An hour and a half after the end of the operation the animal was inactive and appeared to be sleepy. The eyes appeared to be turned from their normal positions, the left especially being turned inwards and upwards. When a finger was put through the wire netting the monkey crouched back into the corner of the cage. When a piece of bread was held in front of the cage the monkey put its hand awkwardly towards the bread, took it and conveyed it to the mouth. Other pieces of bread presented through the wire netting were not taken. A small piece of bread dropped on the floor of the cage was apparently seen, for it was picked up immediately and without hesitation. A piece of banana was presented through the wire netting about 30 cm. from the animal. The left hand was put forward, although the left side was farther from the food, and the banana was grasped in an awkward manner. Other pieces of food were presented and were sometimes taken and sometimes not taken. When they were taken the movements were slow and inaccurate. A short stick thrust through the netting did not cause the animal to make the usual defense movements of grasping and shoving, but the left hand was put forward to take the object. When the stick was quietly inserted into the cage in any direction the eyes of the animal were directed toward it when it came sufficiently near (about 15 cm.), and although the animal did not fight against it as a normal animal did, the eye movements were exactly like those of a normal animal. A white dish containing water was placed in the cage, and the animal soon placed its head in the dish and drank. A second attempt to drink was more quickly made. It was noted as peculiar that the monkey did not use the right hand for grasping, but used the left which performed the movements in an uncertain manner. Previous to the operation this animal usually used the right hand. At the time the notes were made the following question was inserted: How much of the inaccuracy in movement is due to the heterophoria? This question has not been answered and even at present I have no indication of the part this may have played in the motor inaccuracy. Throughout these observations the animal

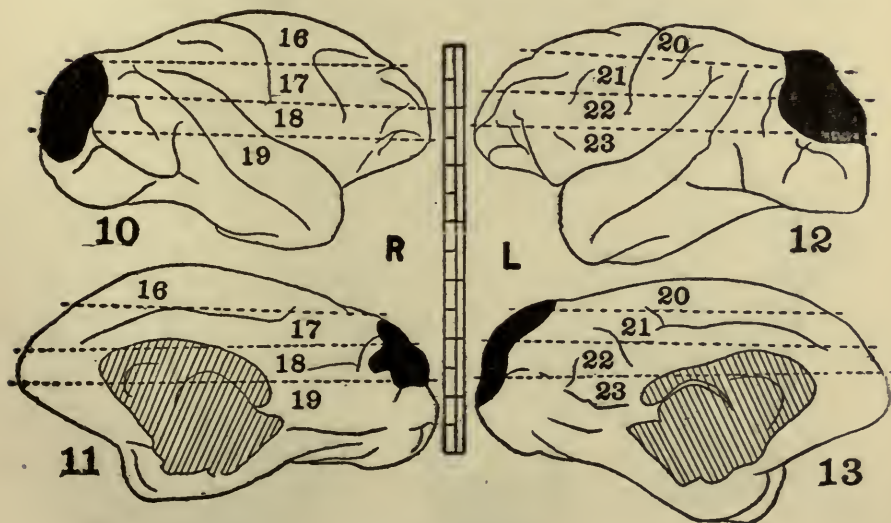
appeared to be under the influence of the anesthetic, to be sleepy, with lack of energy, little attention and a "don't care" attitude.

Twenty-seven hours after the operation the animal seemed perfectly normal, except that his movements were slow and deliberate, and quite unlike the quick sharp movements of a normal animal. Pieces of raw sweet potato were given to him; these he took slowly and put into his mouth only after having smelled them. He ate them in a normal manner. Once a piece of potato was dropped on the floor of his cage, he looked at the food, then at me and reached for the food which he obtained although all the time he kept looking at me. Apparently, the animal had made a judgment of the location of the food, and acted upon this judgment even when the eyes were turned from the food. He drank water from a dish apparently without difficulty, and picked up particles of food from the floor of the cage. When a stick was presented to him he slowly reached out his hand and took hold of it. His attention was attracted by someone in front of the cage and a stick was placed in the back of the cage, care being taken to make no noise, and when the stick came within the field of vision he immediately turned and often seized it. This reaction was the same whether the stick was to the right or to the left. The angle of the stimulus was not accurately determinable, but it appeared that the animal could see objects in the outer portion of each field, i. e., with the nasal portions of the retinae, at least as far away as 70 to 80 degrees. The angle of vision above the head was apparently normal. There was a decided preference for the use of the left hand, but it did not appear that the right hand was in any way paralyzed, although from his continued use of the left it would appear that there was a paresis or some similar change from the normal.

Three days after the operation the animal appeared the same as that just noted. On this day, five tests with the colored breads were made. On the first, second and fifth the monkey took only the red bread, but on the third and fourth tests took both yellow and red. Two days later, five tests were correct. The animal was exhibited before the Georgetown Clinical Society on April 4, and at that meeting the members were unable

to note any difference from the normal. From the results of the bread tests it was apparent that the animal retained the ability to discriminate colors, and although the tests on the third day after the operation were not entirely successful, they were quite as successful as they had been immediately previous to the operation.

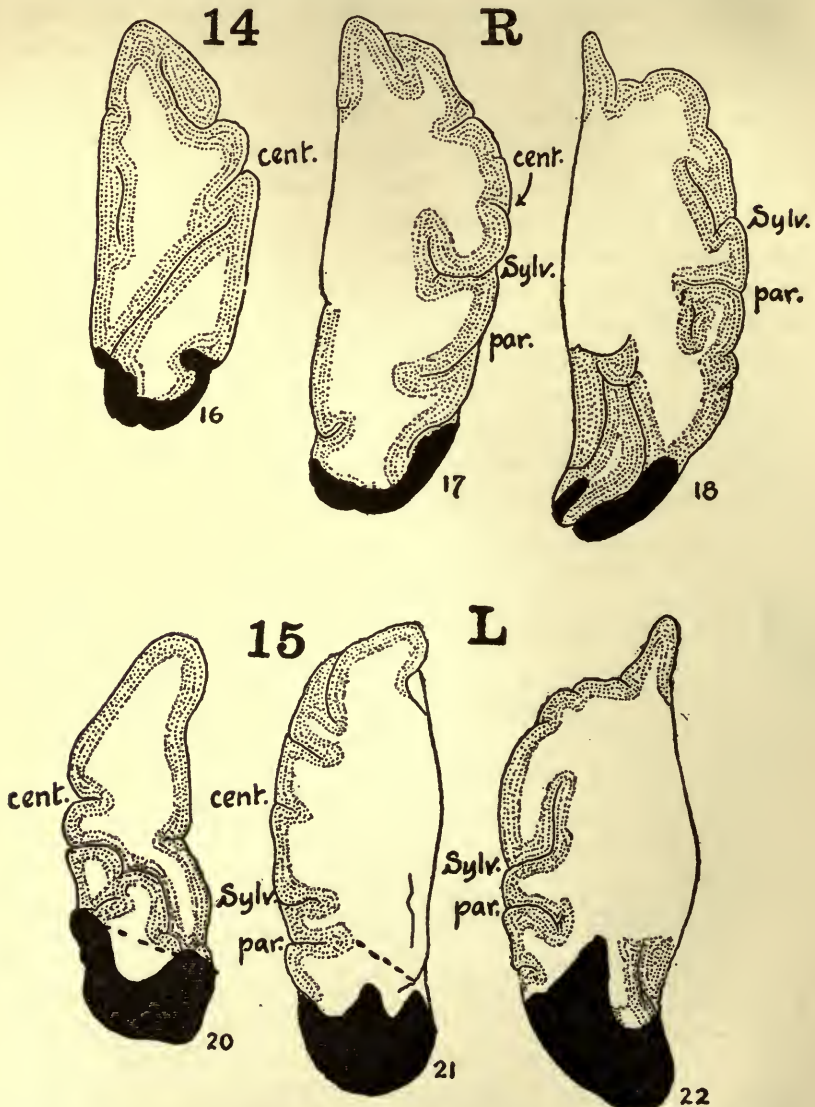
Nine days after the operation (April 10), it was noted that the animal was not inclined to work. It did not eat. During the night of the 9th the animal tore the bandage from the head, and opened the scalp wound slightly. On the following day the scalp was swollen, and the brain appeared to be bulging through the trephine openings. The animal did not work on the tests, and, as it refused to eat, no observations of vision or of movement were possible. At 8 p. m. of this day the animal was found to be quite stupid and dull. It took a long time and a violent stimulus to arouse him. At one time the eyes were rolled upwards and showed a slight nystagmic movement. At another time there were twitchings of the hand. The animal



FIGS. 10, 11, 12 and 13. Monkey 1. Lateral and mesial aspects of the cerebral hemispheres, showing the parts destroyed by the operation. The latter is a reconstruction. Slightly reduced (cf. scale). Traced from photograph. The small size numerals are the sections from which other figures (14-23) were drawn.

was killed with chloroform at 9:30, and the autopsy was performed immediately.

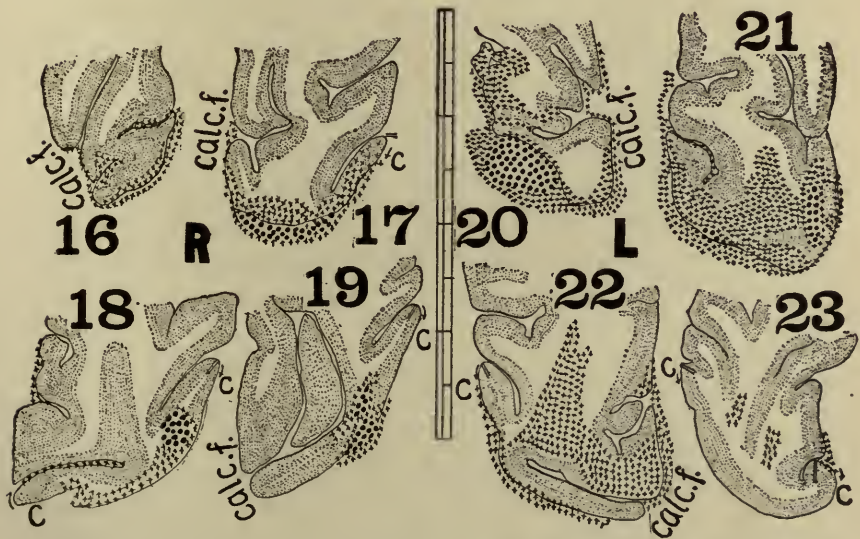
At the autopsy the scalp in the neighborhood of the operative



FIGS. 14 and 15. Monkey 1. Gross sections of the hemispheres, showing the parts affected by the operations. About natural size. Drawn at time of autopsy, free hand. The illustrations are taken from the lower surfaces of the sections indicated by lines in figs. 10-13.

cuts was found to be swollen, the cellular tissue was filled with a watery fluid which could be squeezed from it. The scalp at this place was about a half centimeter thick. The brain bulged through the trephine openings. The dura was adherent to the brain and the scalp was adherent to the dura. The brain was removed from the skull with difficulty. The posterior surfaces of the hemispheres were much reddened and soft to the touch; there was no appearance of pus. The brain was placed in toto in 95 per cent alcohol. The photographs were made thirty-six hours after the autopsy.

Figures 10 to 23 show the brain with the effects of the two operations. In figs. 10, 11, 12 and 13 are given diagrams of the lateral and mesial aspects of the hemispheres, with the parts of the cortex destroyed at the time of the second opera-



FIGS. 16, 17, 18, 19, 20, 21, 22 and 23. Monkey 1. Horizontal sections through the occipital parts of the cerebral hemispheres, showing effects on cortex, and underlying fibers of the second operation. About $3/2$ natural size. Edinger drawing apparatus.

tion. Figs. 14 and 15 show the gross appearance of the sections made for the purpose of microscopical study, with the parts marked thereon where the cortex had been destroyed. The cor-

tical effects of the first operation are not indicated, and it was impossible to differentiate these from the results of the second operation. Figs. 16, 17, 18, 19, 20, 21, 22 and 23 give the appearance of the microscopical sections, which were stained by the Nissl method, and which show the hemorrhagic and cortical effects of the second operation. It will be noted that the sections numbered in figures 10 to 15 correspond with the sections marked with the same numbers in figures 16 to 23. The areas of cortical destruction (marked black) in figs. 10-15 have been drawn from the examinations of the microscopical sections.

The results of the examinations of the microscopical sections are given by Dr. Lafora as follows: "Monkey 1, cauterization of the brain, Nissl method, horizontal sections. On the right side the occipital lobe lateral aspect is almost entirely destroyed, the lesion involving the whole depth of this part of the cortex. A part of the periphery of the calcarine type of cortex escaped destruction, and the calcarine fissure is affected only in its posterior ramification, especially the superior part. On the left side the lesion is more extensive than on the right, the calcarine type of cortex being more affected especially in the superior part of the occipital pole. The vessel lesions have produced softenings in the white matter which interfered with the fibers coming to the visual cortex. The anterior part of the calcarine fissure, and some parts of the posterior are well preserved."

Monkey 2. This animal was trained to discriminate the four colors. Red and blue were sweet and green and yellow were bitter. The training experiments began October 20. There was a gradual acquisition of the habit of taking the red and blue and of leaving the green and yellow, which became perfected (after this date there were no wrong reactions as long as the animal was in a normal condition) after six days. The tests were continued, however, a month longer, with intervals in which the memory was tested. The final tests were made on December 1, the day of the operation, and on this day the animal made no mistakes in ten trials.

Operation, December 1. The usual preliminary parts of the operation were performed in the manner described. On account

of the fact that previous sections of the brains of other animals had not been followed by visual disturbances of sufficient amount to be noticeable, if they were present, I made the incision in the brain much anterior to the so-called visual cortex, so that as much of the occipital pole as possible should be included in the effects of the operation. It was intended to separate completely the occipital lobes from the frontal parts of the hemispheres, but on account of the depth of the brain at the point the knife was inserted, all was not cut away, as was later learned at the time of the autopsy and at the time of the microscopical examination.

About fifteen minutes after the operation was completed the animal staggered drunkenly against the sides of the cage in which he had been placed. When a sudden noise was made he did not jump. The pupils were widely dilated, and there were slight tremors of the eyelids.

Twenty-four hours after the operation, the animal was found to be fairly active, engaged chiefly in pawing at the floor of the cage and scratching at the bandage on his head. A finger of the experimenter poked through the wire of the cage elicited at times a slapping of the floor, at other times it appeared that no attention was paid to it, activity at least not being directed toward the finger. A piece of rubber tubing hung through the top of the cage elicited no reaction until the animal was touched, when he made a slap in that direction. Water was presented in a saucer. The animal put out his paw to investigate, got it in the water, then leaned over and drank. A prune was held outside but near the wire of the cage. The monkey started to put out his hand to grasp it, but struck the wire and did not persist. Later the prune was held in this position again and the paw was put out and grasped the prune accurately. A prune was thrown upon the floor; three grabs were made in the general direction of the prune and each time the monkey missed it by about 7 cm. It desisted. On the following day he groped about the cage, especially on the floor when any noise was made, and did not reach for objects held in front of him, but gave some reactions to things that were held above the eyes. It seemed at times that he saw things held in the upper part of the visual

field. This was not clear, however, for at times he would not pay any attention to the food. When a stick was held close to him, he paid no attention to it as he had previously done, and there were no defense movements to push away the stick. Only when the food was placed near the nose or mouth did he make definite attempts to grasp it, and at times it appeared that his reactions were due more to smell stimuli than to visual ones.

Three days after the operation he was placed in the large observation cage into which he went from the small living box, almost as soon as the door of the latter was opened. A peanut held at the netting of the cage, about 25 cm. away from his head was well grasped and the movement was quickly executed. No hesitation was observed at this time. A dish of water was placed on the floor of the cage about 54 cm. from where he was sitting; the animal immediately went to it, drank from it in an apparently normal manner, and went back to his old sitting position. Other food was placed outside of the cage but within reach of his extended paw, and these pieces he took and ate. Small pieces of food on the floor of the cage were taken in an apparently normal manner, and the sawdust on the floor of the cage was picked over for particles of food. A stick inserted in the cage was promptly seized, and ward off. The animal moved its eyes in an apparently normal manner, and the eyes followed a moving person. The animal turned its eyes toward anyone entering the room. It moved from the large cage to the small one and reversely without mistakes regarding doors, etc., and in this respect also appeared to be able to differentiate visual stimuli.

Four hours later the animal seemed visually like a normal animal. It took food, drank water, and put its hand through the cage to get materials outside. At times its movements were not as accurately coordinated as in a normal animal but the errors of movement were not large and on this point it was impossible to make any accurate judgment. The animal scratched the bandage almost continually and it was thought that perhaps there was some pus formation at the wound. For this reason the animal was lightly anesthetized, the old bandage taken off, and a new one adjusted. The wound seemed to be in a perfectly

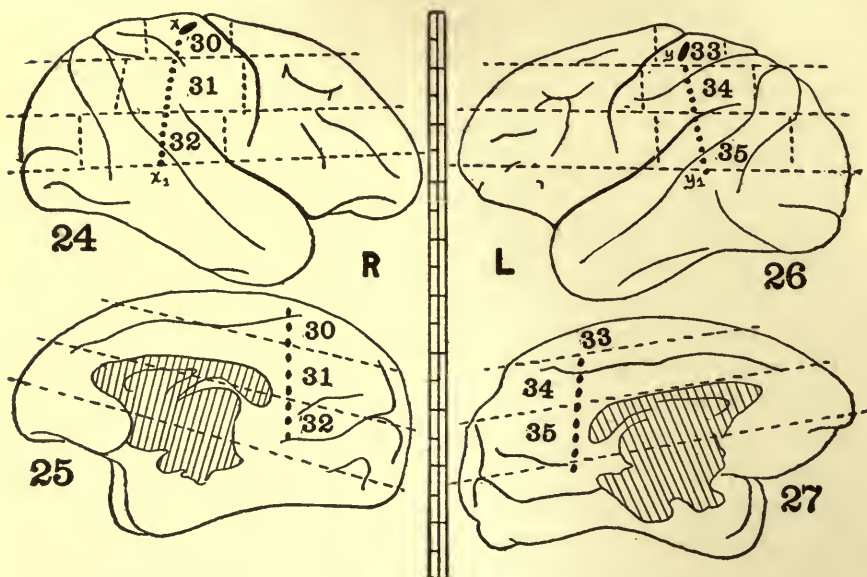
healthy condition, and to be uniting by first intention. A wet compress of 2 per cent carbolic acid was placed on the head over the wound. The animal recovered from the anesthetic in about an hour. The animal moved from the small cage to the burlap bag without any difficulty and apparently knew what it was doing.

On this day and on the succeeding days, the animal appeared to have perfect vision and to be able to coördinate the visual impressions with the proper movements. At no time after the first days was I able to determine any defect of vision, and this was also shown in the tests with the colored breads. Two days after the operation the animal made some mistakes with the colors. In all of the ten tests made on that day the animal took the yellow bread and smelled of it. Once a piece of green bread was taken in the same grab with a red, and this was apparently due to the fact that they were very close to each other on the plate. On the following day, the monkey made no mistakes in the color tests, and it seemed most likely that the mistakes made on the previous day were not due to a lack of discrimination. It is particularly worthy of notice that in one of the tests the piece of blue bread fell from his hand and that he immediately picked it up, rather than take one of the other (yellow and green) pieces remaining on the plate. The observations, and also the tests, indicated that if there had been any visual defect, it was of a nature similar to those observed by Ferrier. The general reactions of the animal were, however, so abnormal for a day following the operation, that I think we are not justified in concluding that the defect is visual and is of any special character, but I believe we should conclude that the disturbance was a general one, and is to be compared with the shock effects of operations such as are exhibited by man, especially after operations on the nervous system.

The animal was killed with chloroform, December 5. The autopsy was performed immediately after death. The brain appeared to be normal except at the points where the knife had been inserted, and there was no oedema apparent to the eye. The brain was placed in alcohol and photographed and weighed

twenty-four hours after the autopsy. The brain weighed 85 grams.

Figures 24 to 35 show the conditions that were found post mortem. In figs. 24, 25, 26 and 27, the tracings from the photographs, there are shown the points of insertion of the knife, and the sections made for the purpose of examination by histological methods. At the time the gross sections were made, drawings were made of the appearances of the sections and these are

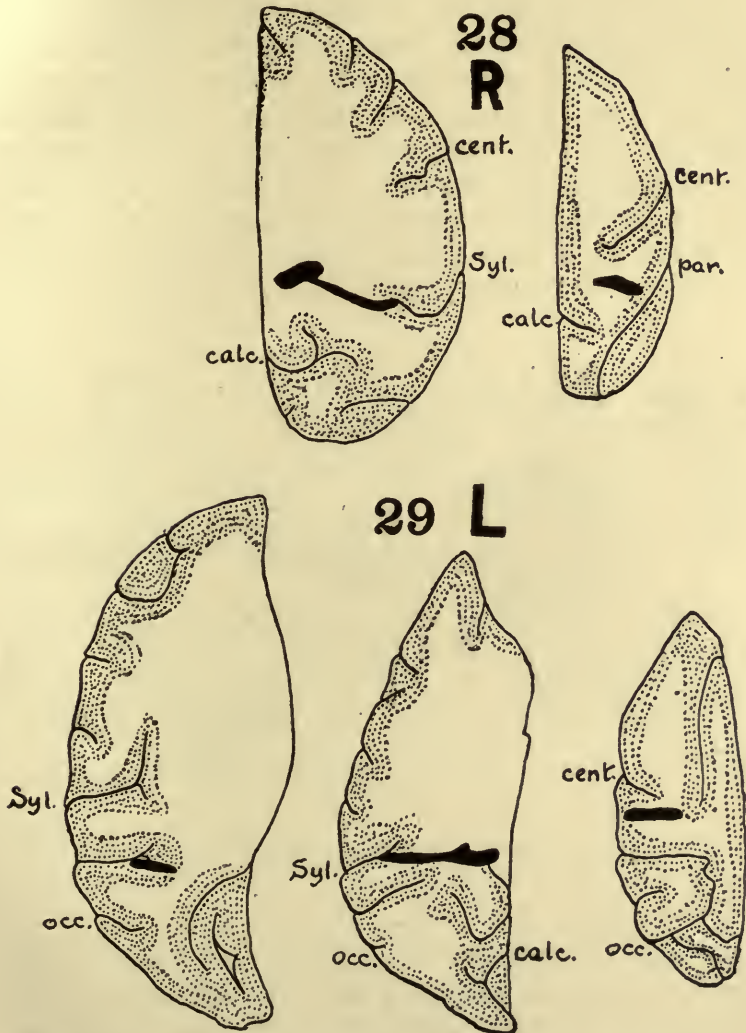


FIGS. 24, 25, 26 and 27. Monkey 2. Lateral and mesial aspects of the cerebral hemispheres, showing the course of the knife cuts into the brain $x-x_1$ and $y-y_1$, and the location of the parts of the brain examined histologically. Slightly reduced (cf. scale). Traced from photographs.

given in figs. 28 and 29. From these drawings and from a careful comparison of the brain as a whole and in the sections, a reconstruction of the course of the knife cuts has been made and these are indicated in figs. 24-27, by the heavily dotted lines. It will be seen that the knife was inserted just posterior to the central fissure and that in its course it cut away a large part of the occipitals from the anterior part of the hemispheres, but that the lower, especially the temporal, portions of the brain

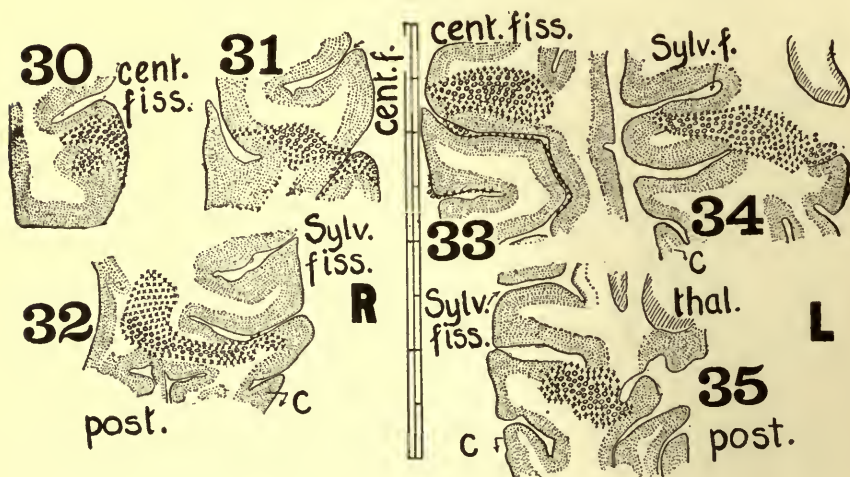
escaped. The microscopical examinations of the sections are illustrated in figs. 30-35.

The account of the histological examination by Dr. Lafora is



FIGS. 28 and 29. Monkey 2. Sections of the cerebral hemispheres showing the hemorrhages due to the sections of the brain, and the parts probably affected by the operation. About natural size. Drawn free hand at time of autopsy. The illustrations are the appearances of the lower surfaces of the sections indicated in figs. 24-27.

as follows: "The sections were prepared by the method of Nissl by Dr. Achúcarro. On both sides of the brain the sections show the lesions produced by the knife, which seem to be very extensive in its transverse directions. Although we are unable to judge of the amount of the fibers which were cut by the operation on account of the histological method used in the examination, it is sure that most of the optic fibers, except those lying low in the cerebrum, were destroyed or at least affected by the section. The cortex shows some reactive processes of the neuroglia and of the ganglion cells some of which later show a slight degree of tigrolysis. In the inferior part of the white matter the lesion is not as extensive as in the middle part. The drawings indicate the general extent of the lesions."



FIGS. 30, 31, 32, 33, 34 and 35. Monkey 2. Horizontal sections through the lesions indicated in figures 24-27. About $3/2$ size. Edinger drawing apparatus.

Monkey 3. This animal had been trained on the discrimination of the large and small pieces of bread. The experiments for the production of this habit were sporadically done, but the systematic training for the present paper was not undertaken until about two weeks before the operation. Following is an account of the process of learning at that time:

September 5, 10 tests: only once ate both large and small

pieces, viz., first trial; on the first, second, third and fifth trials. she took the large before the small, and on the ninth and tenth the large after the small. After the first trial, however, the animal did not eat the large piece, but smelled or tasted it and threw it away. September 6, 10 tests: took the large piece on the first, sixth and on the eighth trials, but ate the large piece only the first two times. September 9, 20 tests: took the large piece only the first two times. September 10, 5 tests: took both pieces the first three trials, but the smaller piece only on the fourth and fifth trials. September 11, 20 tests: first, took both pieces but did not eat larger; from second to twentieth only smaller. September 14, 20 tests: on the first and second trials she took only the small pieces, but from the third to the fifth the larger ones were also taken, although they were only tasted, not eaten. September 15, 10 tests: only the small were taken. September 16, 10 tests: only the small were taken. September 17, 5 tests: only the small were taken. These tests were the final ones before the operation which was begun an hour later.

Operation, September 17, 10 a. m. Occipital lobes were cauterized. There was considerable hemorrhage which was checked by hot compresses to the brain. Immediately after the completion of the operation the face of the animal was cyanotic, the eyelids closed, and the facial muscles were contracted into a grimace (*Schnauzkrampf*). The left pupil was about one and one half times larger than the right, and neither reacted to light. The head was turned backwards and towards the left; the right arm was flexed at the elbow and the left arm was extended; both legs were extended. There was hypertonia, more marked on the left.

About three minutes later the left arm became flexed at both shoulder and elbow and the left leg at the thigh; the flexion of the left arm at this time was greater than the flexion of the right arm noted immediately after the operation and which had continued. When the animal was placed on its back or on the right side there was a tendency to turn to the left, and the trunk of the animal described an arc with the concavity towards the left (*emprosthotonus*). The tongue was protruded, and deviated to the left; when it was pushed into the mouth and towards

the right, it gradually returned to the protruded left position. Ten minutes after the operation was finished it was found that both sides of the animal were approximately equally flexed, and the tail was turned under the body but in the median line. The animal was tremulous; it was placed close to the fire and the tremor (shivering) ceased in about two minutes.

About half an hour after the operation the animal attempted to sit up, but immediately fell down, and remained in a rather unnatural attitude. Two hours after the operation it was found sitting up, and when I moved about the room it followed with its head and eyes all my movements; part of this may have been due to the noise made by me in walking, but the movements of the animal appeared to be rather those associated with vision.

Eight hours after the operation, the animal was sitting in its cage in a perfectly normal attitude. The contractions of the groups of muscles had entirely disappeared, and, so far as could be determined, the movements were normal in character, but rather slow. Four pieces of bread were placed approximately 5 cm. apart on the floor of the cage in the form of an arc, 30 cm. away from the eyes; for about ten seconds the animal took no notice of the food (it had not been fed on this day except at the time of making the final five tests on the discrimination of large and small) but finally accurately reached for and obtained one of the pieces in the middle; after it had eaten this piece it took the second middle piece, but during ten minutes it disregarded the other two pieces which were at the ends. Some pieces of apple were dropped into the cage; some of these the animal picked up with a great degree of accuracy, but the movements were slow and it did not immediately try to secure the food. At times the food was disregarded until some part of the animal, a hand or a foot, touched one of the pieces, whereupon she reached to the appropriate spot, secured the piece and inserted it in the mouth. A fresh fig was placed in the cage about 45 cm. distant from the eyes of the animal. This it disregarded until it was shoved near enough to the animal to be touched by it, whereupon the animal took the fig and ate half of it. After this she wandered around the cage picking up pieces here and there, but at other times her attention was attracted to

the pieces of food solely by the sight, and at times it appeared that the animal did not see but picked up the food only when it was accidentally touched by part of the body. Tests for determining the extent of the visual field were unsuccessful, for the animal did not respond to the food when it was offered on the wires. The latter observations were made at night in artificial, but good light, and it is possible that the shadows thrown by the food on the wires and the shadow of the cage on the food were distracting, although I lay no stress on this point. During all the tests mentioned in this paragraph the right eye of the animal was much inflamed, probably due to the anesthetic.

Twenty-four hours after the operation the animal was observed and tested by Dr. Lafora, who made the following notes: "The right eyelid is much inflamed, but the eye is kept open, and is used with the other; the pupils react equally to light. Objects (food) at some distance (about 60 cm.) were at first not attended to and it appeared that the animal could not see them; only when pieces were brought near its face did it try to take them. In a number of tests she continued to make movements as if to take other pieces of food in the same place although none were being presented; at other times the animal would look directly at the places and moved her head and eyes as if to follow the movements of the (imaginary) particles of food. Is this a perseveration phenomenon? Small objects, such as wires, were not well discriminated, for the animal frequently made no movement until the wires were close to, sometimes touching, the face or the facial hairs; similarly with small pieces of apple. The first experiments on the field of vision indicated that the monkey did not have a normally fine perception in the macula. for objects about 40 cm. away were peered at and the animal moved the head closer as if to get a better view before attempting to take them. All objects held towards the periphery were seen but the movements of grasping were not accurate. It is a remarkable fact, however, that the animal looked at a fly at the bottom of the cage and followed its movements with head and eyes. A piece of an apple was afterwards held on a wire in front of the animal and moved about far and near and to the right and left. The animal apparently centered its attention

upon the object which it approached and obtained after some unsuccessful attempts. After the monkey found it impossible to obtain some moving pieces of food by grasping with the hand, the animal moved the head towards the food and took it directly into the mouth. Pieces of food held to the right or to the left brought about approximately normal movements of the animal, except when the food was held at the extreme right, where it was found that movements were sometimes produced but only after a much longer time than when the food was held in any other part of the field. The hallucinatory tendency, noted above, to take objects not presented was again shown in the later movements; at times when pieces of food had not been presented for a minute or two, the animal grasped in the air or groped on the floor in the location of previously obtained food; this would indicate that the visual part of the reaction is not a perservation but an hallucinatory phenomenon. Color discrimination appeared to be preserved, at least to some degree, for the animal selected tomato three times instead of apple, its normal preference being for the former. In the later experiments the movements of grasping were accurate, showing a complete association between the movements of the hand and arm and the visuo-kinetic representation of the movement. A piece of cotton soaked in alcohol and then lighted was brought close to the animal and this experiment many times repeated showed that there was an ability on the part of the animal to see with all parts of the retina, on the right as well as on the left, the movements in all parts of the field being accurate and quick. When one piece of lighted cotton was shown and held the attention of the animal, and a second piece was brought inwards from the sides (right and left) the animal turned towards the second piece, showing that the extent of the field was approximately normal. Conclusions: Diminution of visual acuity; no diminution in extent of the visual field, at least at the sides, although it is impossible on account of the eye movements to determine whether or not there is a central scotoma; ability to discriminate colors appears to be preserved; and there is exact visuo-kinetic representation."

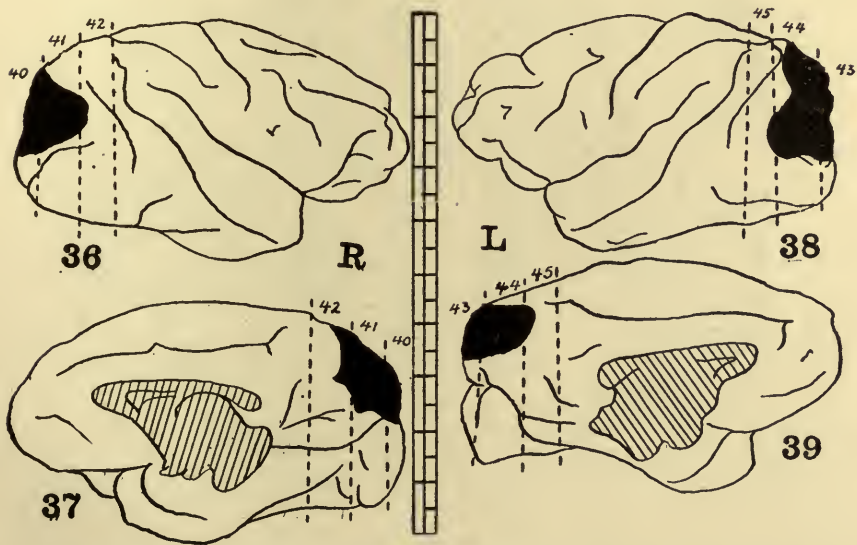
On the third day after the operation the animal was tested with large and small pieces of bread; on the first trial she selected the

small piece and disregarded the large; on the second trial she took the large piece tasted it and threw it away and then took the small piece which she ate; the third trial was a repetition of the second; on the fourth trial she took only the small piece; and on the fifth trial she got both pieces in one grasp and ate the small. The results of these experiments do not indicate plainly whether or not the habit of discrimination of the large and small pieces persisted, but the indications are that the habit remained, because each of the two times that the animal obtained the smaller piece she did not try to take the larger one which remained on the glass plate, and each of the two times that she obtained the larger piece first she returned to the plate and secured the smaller piece. In these experiments she showed the condition noted in the other tests on this day, viz., a certain amount of inaccuracy in motor adjustment. The taking of the larger piece in the fifth trial was awkwardly done, and the taking of both pieces in the second and third trials may have been due to this motor derangement. A piece of raw potato was dropped on the floor of the room close to the cage, about 75 cm. from the animal; she moved to the front of the cage, accurately reached under the bottom bar and secured the piece of food. A piece of raw apple was held on a wire about 20 cm. from the eyes of the animal, and midway between them; this she grasped on the second attempt after having made at first an error of 2 cm. After having obtained the piece of apple she grasped in the same direction (or place) although there was no food being presented, and her actions at this time gave me the same impression as they did Dr. Lafora on the preceding day, viz., that there was an hallucination or a persistence of the impression. A piece of raw potato held in front of the animal about 30 cm. away was reached for; in grasping for it the animal made a movement error of about 7 cm. at first but on the second attempt secured the food. A fly was walking over the back of the cage about 60 cm. from the monkey and to the left; the animal moved cautiously toward the part of the cage where the fly was and when near enough she grasped for it with the left hand, hitting the spot where the fly had been (the fly flying away when the hand approached). A piece of raw carrot was dropped into the cage, but fell outside; the animal groped at

the place where the carrot fell, moved to the other end of the cage, returned to its original position in about ten seconds, and picked up a piece of raw potato; then it put its hand outside the cage and picked up the carrot accurately and without hesitation. A piece of apple and a piece of potato were placed on the floor of the cage about 75 cm. away from the animal; by short steps she moved in the direction of the food and when sufficiently near reached accurately for and obtained the potato but disregarded the apple which was on the right. Nine small pieces of food, three each of raw carrot, apple and potato, were dropped into the cage from the top, a few rolling outside and the distribution in the cage being irregular, the monkey took immediately two pieces which were within reach, then took a step and secured two pieces farther away; after having secured a fifth piece she dropped it before getting it to her mouth and it rolled away about 10 cm. from its original position but she secured it immediately; then she secured pieces of carrot and of apple which had fallen in the shadow; finally she looked outside the cage and secured two remaining pieces which had rolled outside the cage. Two small wads of cotton were dropped in the cage; for a time she disregarded these, but picked up similarly sized pieces of apple and carrot, but finally she picked up one piece of cotton and placed it in her mouth. A piece of sugar was silently placed on the floor of the cage about 70 cm. away from the animal; she stopped trying to pick up the small particles of food near her, made three steps and accurately grasped the sugar; another piece was dropped into the cage and it rolled close to the body of the animal; she peered around but did not secure it, then moved away about 30 cm., turned around, immediately reached for and secured it; a third piece was dropped in the cage in the shadow; for about a half minute this was unnoticed but then she made five steps and with an accurate arm movement secured it. Quick movements of the experimenter's hands and arms in any direction made the animal start and crouch in a corner; fingers and sticks placed through the wire netting were also startling. A piece of raw potato was placed in and stuck by its moisture to the bottom of a glass crystallizing dish, 5 cm. diam., the dish was then placed in the cage bottom side upwards; the monkey reached for the dish,

made the proper adjustment, picked up the dish, turned it in the proper position and tried to get the potato by putting the mouth in the dish; when she could not get the food in this way, she put out her tongue, dislodged the food, secured it with the right hand while the dish was held with the left. A fly on the cage 20 cm. away and to the right was caught at but not secured although the movement was accurate. A small piece of apple was wrapped in a piece of paper and placed 75 cm. away, the package was secured immediately and opened in the usual way by teeth and hands. Similarly with other packages.

The animal was killed with chloroform at 11:30 a. m. so that the brain could be examined before there were any marked extensions of the lesions and before any repair could be brought about.

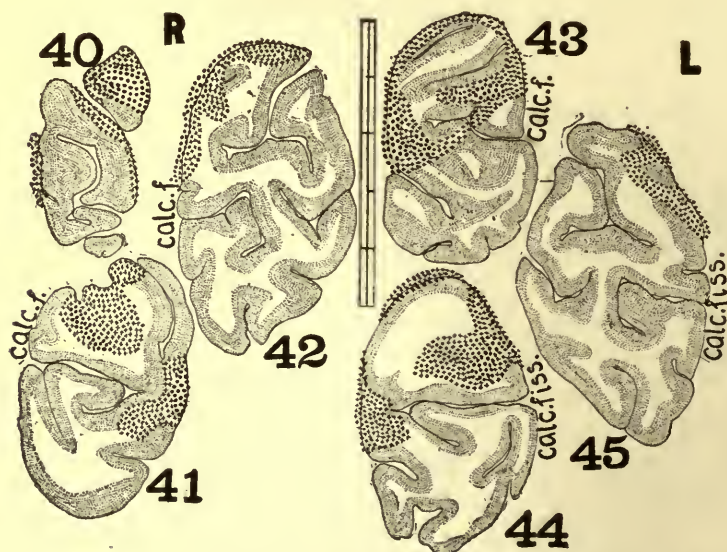


FIGS. 36, 37, 38 and 39. Monkey 3. Lateral and mesial aspects of the cerebral hemispheres, showing the amount of the cortex involved by the operation. Slightly reduced. Traced from photographs.

The autopsy was performed fifteen minutes after death. The wound was healthy in appearance. The brain showed a slight hernia beneath the two skull openings and weighed 102 grams. On account of the brief time between the operation and autopsy,

the brain was examined only for the destruction of cells and the extent of lesion.

Figures 36 to 45 show the amount of the destruction of the cortex. An examination of the microscopical sections (figs. 40 to 45) shows that comparatively large amounts of the fibers were destroyed as well as the cortex, and the cautery undoubtedly penetrated the white substance as well as burning the cortex. It will be seen that the cortex in the neighborhood of the calcarine fissure has entirely escaped, and remained normal, while the greatest amount of destruction took place over the convexity of the hemispheres, being more marked over the superior portion.



FIGS. 40, 41, 42, 43, 44 and 45. Monkey 3. Microscopical findings after the cauterization of the cortex.

The report of Dr. Lafora on this case is as follows: "Monkey 3, Nissl method, frontal sections. On the right side the destruction of the calcarine type of cortex was fairly complete towards the occipital pole except along the calcarine fissure. The calcarine fissure is affected only in its profundity by a reactive process which arose from the injury to the external part of the hemisphere. On the left side the lesions are a trifle more exten-

sive, but the calcarine fissure is affected only in its extreme depth. The external part of the lobe is almost entirely destroyed."

From the accounts of the histological findings and of the clinical appearances of the monkey following the operation, it is plain that the visual defects are not in proportion to the amount of destruction of the so-called visual cortex, and that the lack of blindness can not be ascribed to the failure to destroy the part of the brain which is supposed to have visual functions. This case is to be compared with that of monkey 5, in which latter the calcarine fissure was destroyed more than the remainder of the visual cortex, and the clinical accounts of each of these monkeys differ to an extent to be paralleled by the microscopical findings.

The animal retained its visual function to a very great degree and the disturbance in function can be said to be almost exclusively a dissociation between the sensations from the eyes and the movements of the hand (and other parts). The observations do not indicate a visual defect *per se*.

Monkey 4. This animal had been trained by Dr. Shepherd in his experiments, and about eight months later for a period of about nineteen days it was trained to discriminate blue (sweet) from green (bitter) and yellow (bitter) breads. At this time the habit of taking the blue and leaving the green and yellow was firmly established. No further experiments were done for about seven months at the end of which time the animal appeared to have almost perfect retention of the habit and reacted properly to the conditions as is indicated in the accompanying account.

July 30, 5 tests; in the first test the monkey took the piece of blue bread at first and then the piece of green, but threw the latter away without eating it; the fifth test on this day was made with two pieces each of the three colors arranged in an irregular order and the animal took only the blue breads. July 31, 3 tests; in all tests the animal took only the blue bread; but did not pay any attention to the foods after the third test and the series could not be continued on that day. August 7, 5 tests; in all these tests, after the interval of seven days, the animal took only the blue bread; at first it did not work rapidly but looked around and paid no attention to the breads for several minutes after they

were placed before it; twelve pieces each of blue, yellow and green were arranged on a board in an irregular order and presented to the animal which, after intervals, took ten of the blue pieces and disregarded the yellow and green. August 16, 5 tests; in all the tests the monkey took only the blue bread; in an additional test in which five pieces each of blue, yellow and green were presented at one time the animal took only the blue; it is worthy of note in connection with the discussion of color vision that in the last experiment the yellow bread had been colored by a solution of lead chromate instead of the usual methyl orange, with which it had been previously tested.

Operation, August 17, 2:30 p. m. On the right side an attempt was made to cut away the occipital pole from the rest of the cerebrum by means of the cataract knife; on the left the mesial aspect was cauterized and the cautery was thrust inwards and forwards. The hemorrhage was considerable on the right side, but it was checked by the application of 1:1000 suprarenal solution and by hot sponges. The animal remained lethargic for some time after the operation, but at 4:30 p. m. it was found sitting up in its cage, apparently alert and bright. He appeared to see a hand threatening him no matter from which direction the hand was approached. At 7 p. m. I found the animal had torn the bandage away; after washing the head thoroughly with bichloride, 1:500, I replaced the gauze dressing and bandages and thoroughly sewed them together. An hour later the animal was quiet but appeared to see a small stick thrust at him from right, left, above and below for he moved away from the stimulus.

About twenty hours after the operation, the animal was found quietly sitting in its cage. A piece of bread placed on the floor of the cage was not noticed for about three minutes, but at the end of that time the animal moved toward it, made an accurate movement, picked it up and ate it. A dish of water was placed in the cage, and he immediately moved near the dish, put his head down and drank. Four small pieces of food, one each of bread, cake, boiled potato, and cantaloupe, of about equal sizes were placed on the floor of the cage; the animal selected the cantaloupe first, then took the cake and the potato and left the bread. In four similar tests, the same result was obtained, but it was noticed

that at times the monkey took the bread but threw it away without attempting to eat it. The movements of grasping were usually made with an error of about 3 cm. In these experiments the animal did not always take the food in its hand from the normal sitting posture, but usually lowered its head toward the food before reaching for it. It was concluded that this indicated an impairment of vision, and the inaccuracies in hand adjustments for the grasping of food were taken as confirmations of this conclusion; the impairment seemed to be not a blindness, but only a dimness of vision.

Twenty-six hours after the operation. Two sticks were simultaneously introduced into the cage, one to the right and the other to the left of the animal; that on the right attracted the attention of the animal and was seized, that on the left was not seized even when it was advanced to within a few inches of the head of the animal. One of the sticks was held near the floor, the other above the level of the eyes; the animal reached for the upper stick and disregarded the lower one until it had been moved so as to touch the body. The movements of grasping the stick on the right were as accurate as before the operation, those of grasping the stick above the level of the eyes and those near the floor were very inaccurate. The colored breads, when presented to him, were disregarded and the test of this visual function was unsuccessful. The animal was able to see food and other objects on the floor of the cage but it was not determined in what manner this was accomplished. From the peculiar movements of the head, the lowering and the turning, it appeared to be necessary for the animal to get the visual image on the lower retinal segment, for, although an object lying on the floor was approached, it was not taken until the head had been lowered and the eyes turned downwards. The direction of the errors (right and left) in taking the food were not recorded.

Two days after the operation, the animal went into the small observation cage as soon as the door was opened. At that time the animal was more lively than it had been and its actions were apparently normal. It picked up food lying upon the floor of the cage. When the hand was held above the cage the animal showed signs of fright, shrinking into a corner, etc. A piece of

pear held above the level of the eyes was seized quite accurately. Two pieces of pear were held simultaneously on a level with the eyes, one to the right, the other to the left, each about 10 cm. in front of and to the side of the median line; the animal always took the piece on the left first, sometimes with the right hand, sometimes with the left. A rod and a piece of pear were held simultaneously in the upper part of the field; when the rod was on the left it was seized and the pear was disregarded; when the pear was on the left it was seized and the rod disregarded. A rod held about 15 cm. below the level of the eyes was disregarded until the head was moved or until the rod touched the body or the hair. The animal peered through the opening at the back of the cage with all the appearance of the investigation of a normal animal.

On the same day, four hours later, the animal was tested and examined by Dr. Lafora, who reported as follows: "Pupils react well to light. Held yellow and blue breads before the animal twice, and each time the animal took the yellow bread first and the blue afterwards. A piece of melon and blue bread, the latter nearer the animal were presented simultaneously, and the monkey reached beyond the blue bread and took the melon. Two pieces of melon (one held in the visual axis and the other to the right, left, superior or inferior) were presented simultaneously, and each time the animal took both pieces, apparently seeing with all parts of the visual field. For testing the ability to see in the lower part of the visual field a board was placed near the bottom of the cage so that food in the hand could be kept out of sight until it was time to show it; in the right hand a piece of food was held in front of the animal in order to attract the attention, but just beyond the reach so that the animal would need to exert himself in his efforts to obtain the food, and a second piece was held in the other hand behind the board; the attention of the monkey was gained by the exhibition of the piece of food in the right hand, but when the second piece was exposed, the animal reached for the latter. Two tests were made with pieces of green and white breads after having performed many tests with melon and white bread; in the later tests the animal always reached for the green bread; in tests with green and blue breads in which the green

bread was held nearer the animal than the blue, the monkey always reached beyond the green bread and selected the blue bread. When, however, the blue bread was held in the inferior and the green in the superior part of the field the green was always taken. When a piece of melon and a piece of green bread were shown simultaneously the animal always selected the green melon. Under the following conditions the animal always selected the vegetable or fruit instead of the bread; blue bread and tomato; blue bread and melon; green bread and tomato; green bread and melon; even when the bread was nearer or farther from the animal, to the right or to the left, and when one or more pieces were presented simultaneously. Repeated tests to determine whether or not both right and left visual fields were normal showed that the animal made grasping movements for food regardless of the part of the field in which the food was presented, but that the movements for food on the right were not as quick as those on the left. When pieces of melon or tomato were held in the hand close to the cage the animal always took them, but did not take the green, red or yellow breads."

Four days after the operation. When a plum was thrown into the cage the animal moved toward it and tried to pick it up but failed several times to locate the fruit. At first it grasped another piece of food which it then smelled and rejected, and continued to seek the plum until it was found.

Five days after the operation. A paralysis of both hands was found, the fingers were shut into a fist and there was a wrist drop. The movements of the arm appeared to be normal, and it was found that when the arms were extended the fingers were voluntarily moveable to a slight extent. When a pear was rolled on the floor of the cage the animal moved toward it and attempted to get it in his hands but on account of the flexion of the fingers could not do this; the pear was then eaten by the animal moving its head close to the pear. The pear and other pieces of food were held to a slight extent by the thumbs of both hands, which appeared to be more moveable than the fingers.

On the following day (six days after the operation), the paralysis of the hands disappeared; the movements of grasping and of holding were normal in character, and, judging from the force

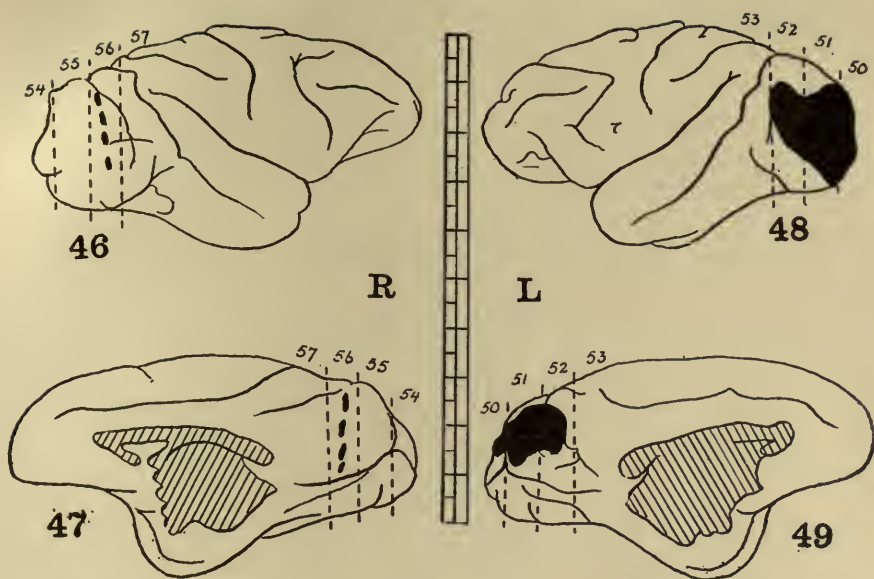
with which it held a rod inserted into a cage, of good force. The monkey did not eat any bread presented to it, and the colored breads were disregarded; on this account a test of the color discrimination could not be made. All fruits and vegetables were rapidly and unerringly selected from the food presented to him so that it was evident the animal had considerable discrimination ability. The animal was not fed at this time and in the afternoon tests with the colored breads were made. In two tests the monkey selected the blue bread and disregarded the yellow and green, but on the third test the animal picked up at one time both the blue and the green, disregarding the yellow.

Two days later (eight days after operation). Tests with the colored breads; in three tests took blue bread and in the third took yellow after having eaten the blue, but did not eat the yellow; in a fourth test in which two pieces each of yellow, red and blue breads were presented simultaneously in irregular order, the monkey took the blue pieces, brushed the red pieces off the plate and disregarded the yellow bread. Tests with small pieces of bread, cooked potato, raw apple, cooked green beans, and raw tomato resulted in the selection of the vegetables and the disregarding of the bread.

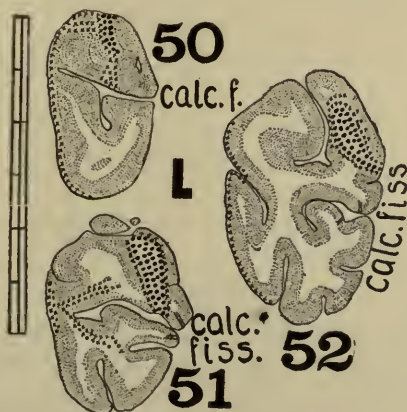
Ten days after operation. The animal was found in a convulsion with twitchings of arms, head, eyelids, etc. The fingers were flexed as they had been five days previously, and there was inability to grasp food; the condition passed away by the following day, and the animal caught with accuracy grapes rolled toward him on either side and placed them in his mouth. Other foods were selected from bread, their positions were accurately judged (as evidenced in the accuracy of the movements) and they were eaten.

Five days later (fifteen days after the operation). Color tests; took only blue bread. The animal was killed on this day in order that examinations of the brain might be made by the methods of Marchi.

Figures 46 to 57 show the results of the post mortem examinations. In figs. 46 to 49 are shown the results of the lesions. The extent of the cortex destroyed by the cautery was accurately determinable but on account of the character of the operation on

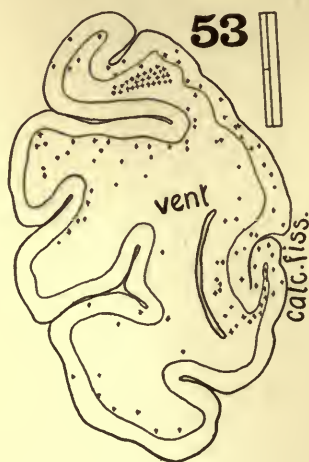


FIGS. 46, 47, 48 and 49. Monkey 4. Lateral and mesial aspects of the cerebral hemispheres, showing the extents of the lesion of the cortex on the left side, and the approximate course of the knife cut on the right. Slightly reduced. Traced from photographs.



FIGS. 50, 51 and 52. Monkey 4. Frontal sections of the left hemisphere in the neighborhood of the cauterization, showing the amount of destruction. Slightly enlarged. Drawn with Edinger projection apparatus.

the right side it was not possible to determine the amount of the visual area involved by the operation. The approximate location of the knife cut on the right side is shown in the figure. The results shown in figs. 50, 51 and 52 are due to the cauterization of the cortex, and have been investigated by the Nissl method. In parts it will be noted that the depth of the cortical destruction

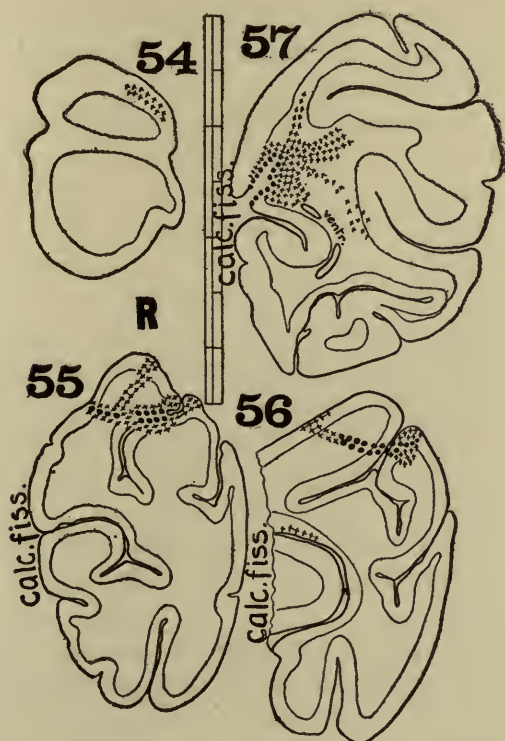


FIGS. 53. Monkey 4. Vertical section through the left hemisphere, anterior to the cauterized area. Few fat drops are indicated in the diagram by crosses. Slightly enlarged. Edinger drawing apparatus.

has not been great, a matter which has been considered in an earlier portion of this article. The section of the left hemisphere anterior to the parts examined by the Nissl method was examined for fiber disintegration, or degeneration, and this showed, figure 53, a rather diffuse process, but with no marked evidences of degeneration. The examination of the right hemisphere by the Marchi method was unsatisfactory, for the only effects of the lesion were those in the immediate neighborhood of the cut.

Regarding these preparations Dr. Lafora has written: "Monkey 4. Cauterization of the left hemisphere, cutting of the white matter of the right hemisphere. Frontal sections. Nissl method on the left, and Marchi method on the right. On the left the calcarine fissure has almost entirely escaped destruction. The outside of the brain (the calcarine type of cortex) is affected in the external layers up to the granularis interna. (On account of

the time of death so soon after the operation the cortex showed only the primary effects of the operation and not the secondary ones.) A large hemorrhage extends over the calcarine type of cortex on the lateral aspect of the hemispheres and extends into the white substance. Sections of the brain anterior to the cauterized area were examined by the Marchi method, and these showed some fat drops as are illustrated in the figures. The right side was placed in toto by mistake into the Marchi fluid which pro-



FIGS. 54, 55, 56 and 57. Monkey 4. Frontal sections of right hemisphere, showing destruction in the neighborhood of the knife cuts. For fuller description, see text. Slightly enlarged. Edinger drawing apparatus.

cedure did not permit a proper impregnation, consequently the appearances found in the sections are only those near the surface. Here are found many fat drops around the hemorrhagic areas, which were produced by the cutting."

Clinically, it appeared at first as if this animal had a visual defect but later observation failed to indicate this, and the conclusion is forced upon us that if there was a defect during the first few days it was minor in character, and not of sufficient amount to be called amblyopia, hemianopsia, or anything more than what Loeb has called a "reduction in irritability."

Monkey 5. In the preliminary experiments this animal had been trained to take red and blue breads and to disregard the yellow and green. These early experiments were made on eighteen days over a period of sixty-one days, the habit being established after five days' experimentation. No further experiments were made for eight months.

August 19, 4 tests; took red, blue and green the first test; red and blue the second test, and only blue the third and fourth tests. August 20, 5 tests were made with only red, yellow and blue, and in all the tests the animal disregarded the yellow. August 23, after an interval of three days, 10 tests were made with blue, yellow and green. In the first test the animal took the yellow as well as the blue, but in the other nine tests took only the blue. August 25, 10 tests; took only the blue and disregarded the yellow and green. On the last two days one test each was made in which two or more pieces of each of the three kinds of bread were presented simultaneously, and in these tests the animal selected the blues from the other colored breads.

August 26. Operation. Both occipitals were cauterized, the cautery being inserted into the brain substance as well as being passed over the cortex.

Three hours after the operation the animal appeared to be fairly normal. He picked up pieces of apple placed on the floor of the cage, the color of which was quite similar to that of the food. The movements were accurate when the food was placed within 30 cm. of the animal, and in addition the animal made accurate movements to secure food held at the top of the cage.

Four and a half hours after the operation, the animal was observed by me in conjunction with Dr. I. W. Blackburn. At this time the following notes were made: The pupils reacted to light in a normal manner, and the general appearance of the animal was normal. He peered around the cage and through the opening in

the back, and examined all things placed in his way. In his usual manner to strangers, he threatened Dr. Blackburn, but afterwards remained huddled in a corner, but moved whenever the hand was inserted into the cage or when food was presented. Grapes rolled toward the animal were immediately and accurately seized; grapes held in the hand 30 cm. distant were reached for but not accurately grasped, for at times he took hold of the experimenter's finger. A grape rolled to the other end of the cage (75 cm. distance from the animal) was disregarded for ten or fifteen seconds, although the animal was hungry and ate anything placed within its reach. Grapes and pieces of apple placed near enough to be reached were easily grasped, but at times with slight incoördination amounting to about 4 cm. The grasping movements were sometimes to one side, at other times to the other, and often nearer the animal than they should have been. A mirror placed in the cage attracted the attention, the animal moved toward it, peered into it and examined the front and looked behind it repeatedly. He took a piece of red colored blotting paper and inserted it into the mouth, but then rejected it. A small piece of bread about 3 mm. in diameter was picked up from the floor, but as he continued to fumble for food and at times picked up grape skins which he had previously rejected it was impossible to decide whether the small piece of bread had been seen or had been hit by the hand as the animal moved the hand over the floor. The monkey repeatedly took the grape skins which it had previously rejected, placed them in the mouth and immediately spat them out again. A pair of eyeglasses were held so that four images of the electric lights were thrown on the floor of the cage; these attracted the attention of the animal and he moved his head and eyes in accordance with the movements of the images.

Four days after the operation. It was noted that when food held on wires was presented to the animal, the food held in the upper left visual field was always seized immediately, but that the food held in other parts of the field was sometimes seized and sometimes not seized. On this day an attempt was made to test the memory for colors but the animal would not touch the breads and the test could not be made.

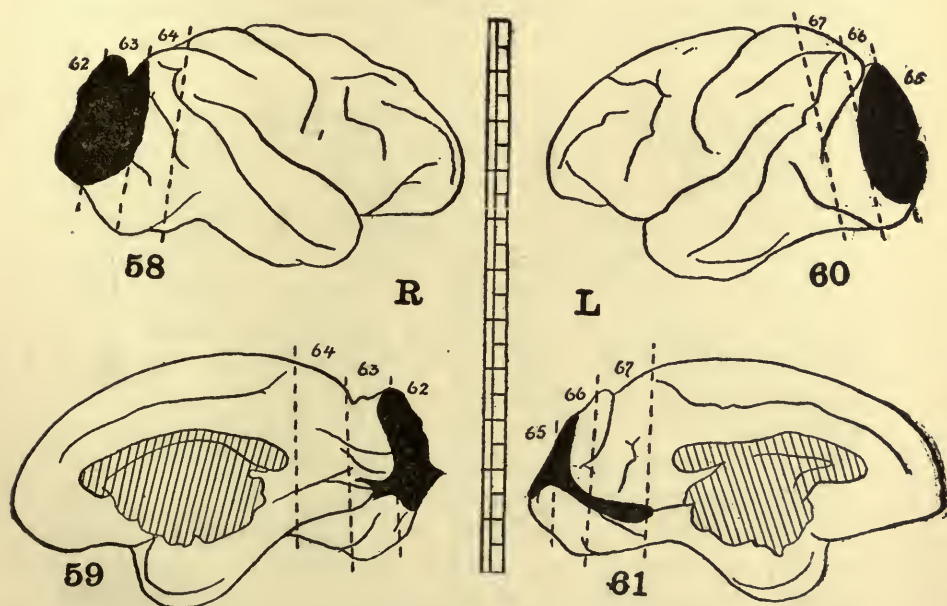
On the following day, five days after the operation, the tests.

with colored breads on the glass plate were also unsuccessful, and the breads were therefore presented in pairs on wires, viz., blue and yellow, and blue and green. In ten tests with the yellow-blue pair the monkey took the yellow once, the blue four times, and both pieces five times. The latter result was obtained after the other five. With the green-blue test, the monkey took the blue five times, and did not take the green. On this day a lump of sugar was placed at the bottom of the cage but it remained unnoticed although before the operation the animal was very fond of sugar. Other pieces of food on the floor of the cage were also disregarded, although when food was placed close to the nose it was seized and eaten with eagerness. A broom and a stick, of which the animal was normally afraid, were introduced into the cage without producing any reaction on the part of the animal.

Six days after the operation the tests with colored breads were more successful. Five tests were made with the following results: In the first test the animal reached in the direction of the blue, but slowly drew its hand backwards and then put its head down to the food plate and took the blue in the mouth. In the second test, the animal fumbled about the plate, finally hit the yellow bread, which it placed in its mouth but immediately spat out. In the third test he grabbed for the bread, caught the green piece, which was tasted and thrown away, and then he took the blue which he ate. In the fourth test, he took the blue bread immediately, ate it and disregarded the other two pieces. In the fifth test he took the blue, but only tasted it; the other pieces were not touched. Following these experiments he was placed in the cage with another animal. As soon as he got into the other cage he walked half way across the cage and picked up a piece of food lying on the floor, and then stood up and reached for a piece of apple on the wire netting at the top. Small pieces of apple were then placed at the top of the cage to the right or left of the animal, and in every case he accurately reached for the food. In one test in which two pieces were placed about 10 cm. apart, he reached for one piece, but in taking hold of the netting the apple dropped to the floor of the cage whereupon he immediately changed the direction of the movement and secured the sec-

ond piece. After having secured the second piece he accurately reached for and secured the first piece which had fallen to the floor.

During the next three days the inaccuracies in reaching for food increased, until the animal was able to get food only by fumbling around on the bottom of the cage. Eventually his movements became like those of a blind person. Ten days after the operation it was noted that the animal had all the appearance of being blind. He paid no attention to the movements of the experimenter's hand and arm or to a small flag. Food held at a distance of 30 cm. was unattended to except when held in the upper left part of the visual field. He reached for food when it was placed on the floor of the cage but the movements were inaccurate and it appeared that the animal did not appreciate

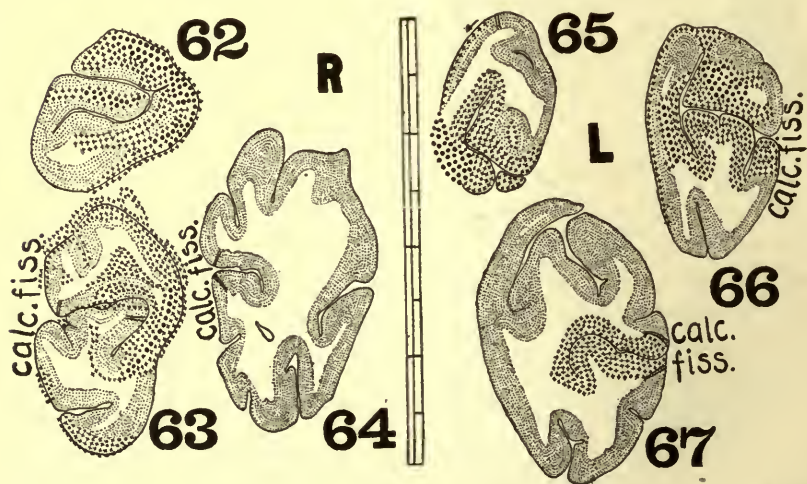


FIGS. 58, 59, 60 and 61. Monkey 5. Lateral and mesial aspects of the cerebral hemispheres, showing the extent of the lesions produced at the operation. Slightly reduced. Traced from photographs.

what he was reaching for. Once a small bright red tomato about 2 cm. in diameter was exhibited in the upper left part of the field;

the monkey reached for it in a fumbling manner and knocked it down so that it rolled to the left and behind him. He sought for the food through the bars of the cage, although none was visible, and groped hither and thither. When the tomato was shown a second time in the upper left field, he reached for it, making an initial error of about 10 cm., but finally managed to secure it. Black and white grapes rolled on the floor of the cage were not taken although the animal seemed eager for food. Grapes held near his nose were taken hold of accurately. In the tests made on this day it should be mentioned that there was an intention tremor and part of, if not all, the inaccuracy of movement, may have been due to this motor derangement.

Eleven days after the operation the animal was tested, and found to be in almost the same condition as that noted in the preceding paragraph, except that there was less ability to grasp things presented to him. He was killed on this day. At the



FIGS. 62, 63, 64, 65, 66 and 67. Monkey 5. Frontal sections of the cerebral hemispheres, showing the parts affected by the operation. In 64 no lesion was found. Edinger drawing apparatus. Slightly enlarged.

autopsy the brain was found bulging above the level of the bone, the hernia on the right side being more marked than that on the left. There were adhesions between the brain and dura and scalp. The brain weighed 92 grams.

The results of the post mortem examinations in this animal showed much more extensive lesions than in any other animal upon which I operated. The visual defect was noticeable only after four or five days (although there was some incoördination from the first) and in this case it is apparent that the end result, the apparent blindness, must have been due to the extension of the effects of the primary lesion. Only the anterior part of the calcarine fissure on the right side was preserved (see figs. 59 and 64) and the preservation of this, with the apparent lack of foveal vision is against the hypothesis of Henschen.

The results of the histological examination by Dr. Lafora are as follows: "Monkey 5. Cauterization of the cortex. Frontal sections, Nissl method. On the right side, with the exception of the most anterior portion of the calcarine fissure, which is a very small area, all of the calcarine type of cortex has been destroyed, even the external part of the occipital pole, and large parts of the white substance in the neighborhood of the calcarine fissure. On the left side the lesion was apparently selective, for the effect is localized along the calcarine fissure throughout its entire extent, and into its depth. The occipital pole has only the outside part of the cortex destroyed."

Monkey 6. This animal was trained to discriminate red and green breads. The training results were as follows:

August 22, 5 tests; in all tests the animal took both kinds of bread. August 24, 10 tests; after the first four tests the animal did not eat the green, although on the sixth test she picked it up but discarded it without smelling or tasting. August 26, 5 tests; in all of which the red was taken and the green was not taken. August 27 and 28, 5 tests each day; in all the green was disregarded and the red taken. August 31, 5 tests; took only red although in the last test on this day four pieces of red and six of green were presented simultaneously. September 1, 5 tests; in all of which the red was taken and no green. On this day the operation was performed.

Operation, September 1. After the trephine buttons were removed the openings of the skull were enlarged by means of bone forceps so that all of the lateral parts of the occipital lobes were exposed. At the time of the operation the hemispheres were

separated by a glass spatula and the internal aspects of both hemispheres were cauterized as well as possible. The injury in this animal was apparently more extensive than in animals 3, 4, and 5. A hemorrhage from one of the large occipital arteries was checked by an application of suprarenal, 1:1000.

A half hour after the operation the animal was found sitting in its cage, apparently looking at everything passing, for she followed me with her head and eyes when moving around the room.

Two hours after the operation, she was found peering through the opening at the back of the cage, and when I quietly moved toward this part she retreated to the other side of the cage. When I was seated in front of the cage and made movements with my hands and arms, she followed with her eyes all the movements in a perfectly normal manner. The reflexes of the pupils were normal. Four pieces of white bread were put into the cage, the animal appeared to look at these, and she touched some and carried one to her mouth, but did not eat it. A grape rolled into the cage among the pieces of bread was instantly seized and placed in the mouth. Three grapes were placed among the bread and all were selected and the bread disregarded; in these tests it was noted that the error of movement was from one to three cm. Pieces of muskmelon were selected unerringly from the bread of the same sizes. Only two pieces of pear were taken although six were placed in the cage. When pieces of melon, bread and pear were presented the monkey took the pieces of melon and left the bread and pear, and when grapes, melon, pear and bread were presented she took only the grapes.

Five hours after the operation she was observed by Dr. Lafora, who made the following observations: "Color vision was tested by the ability of the animal to discriminate foods of different colors; red bread from a red grape, melon from green bread, and combinations of different kinds of food. In these experiments the monkey took the fruit in preference to the bread, but she did not appear to be hungry and after about ten minutes would not attempt to secure food. Tests of peripheral vision by means of food placed at the ends of wires showed that when the food was in any part of the visual field it attracted the attention of the animal and there were no results that could be taken to indicate a

contraction of the visual field, nor any difference in sensation ability."

One day after the operation, when sitting quietly in front of the cage observing the actions of the animal, there being no food in the cage, I saw her make a quick movement in the air thereby catching a fly on the wing. At this time, the monkey did not work with colored breads, entirely disregarding them as they were presented on the glass plate. Throughout the period of observation on this day, the animal kept picking at the edges of the bandage and when she had managed to get a small piece of cotton she would hold it about 10 cm. in front of her eyes, as if carefully examining it; at times she placed the cotton in the mouth and eventually threw it away.

During the next five days there were no new observations worthy of note, the animal appearing to be in much the same condition as was noted the day following the operation. On the sixth day after the operation it was first noted that the animal did not appear to see objects placed on the floor of the cage for she left fruit and other kinds of food although she appeared to be hungry and took all things presented to her in the hand or on wires. On this day the visual defect was like that of many of the animals, indicated by an inaccuracy in movements in grasping the particles of food, for the errors in movement amounted to from one to four cm. On this day, however, four tests with colored breads were made, and in these tests she picked up the red bread and disregarded the green three times; and in the fourth trial she moved in the direction of the red but managed to pick up the green which was only two cm. away from the red.

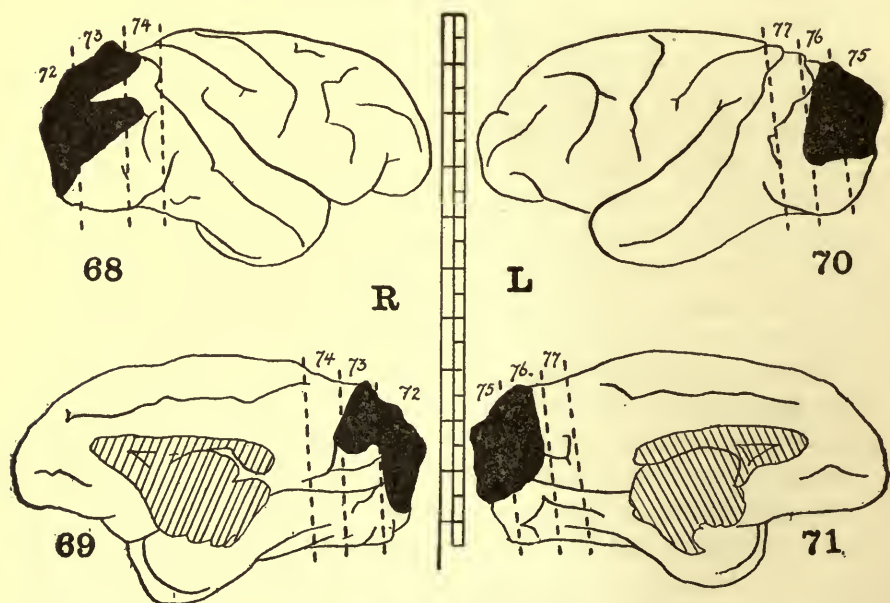
Two days later, eight days after the operation, three grapes were dropped into the cage; they rolled into positions forming an irregular triangle with the apex about 50 cm. from the eyes of the animal. The monkey made repeated efforts to obtain the grapes but at first got its hand 15 cm. too close to its body and then fumbled around until she by chance hit one of the grapes; this grape rolled closer to the animal but the monkey continued to feel around in the spot at which the grape had been felt and at this time she did not manage to get this grape or the other two which were presented. Afterwards with considerable fum-

bling she secured the two grapes the positions of which had not been disturbed and finally the one which had been moved by her fumbling, and which, as has been said, rolled closer to her body. A second set of observations were made on this day with somewhat similar results. The defect of vision appeared to me to be general and not of any particular retinal segment. When two pieces of food were held on wires one to the right and the other to the left, or one above and the other below the line of regard both pieces were secured, but only after considerable fumbling and after making numerous futile attempts to reach the food. Grapes rolled into the cage were searched for and secured only after they had been hit by one of the fumbling hands in their apparently rambling movements. Seven lima beans were placed on the glass plate in the form of a hexagon, and only after much fumbling were these obtained. A small very bright red tomato, placed 60 cm. from the animal, was not noticed for two or three minutes, but after that time it appeared to me that the animal had sensed its presence, whereupon she began a search for the tomato finally securing it after about 40 seconds. Grapes and beans lying outside the cage were secured with difficulty; usually the animal made a movement in the general direction of the food and then, not finding it, swung the arm and hand until something was touched. In taking food presented at the ends of wires and from the floor it was noted that the first movement was in the general direction of the food, and when the food was not secured by this first movement (as was usually the case) the monkey drew the hand backwards, peered at the food for a second or so and tried again. The errors of movement (i. e., the distance between the food and the tips of the searching fingers) averaged about 2 cm., and the record of nine different attempts show that these errors were in all possible directions, too far from, too near, to the right of and to the left of the food.

On the succeeding days the inaccuracies in adjustment became less noticeable, and thirteen days after the operation they were to be discovered only by careful observation. On this day the animal was examined by Dr. F. M. Barnes, Jr., who wrote the following notes; "The animal is quite active, moving about the cage and taking notice of all about it. She does not seem especial-

ly frightened but moves quickly at very slight noises. It seems impossible to make the slightest movement in front of the cage without attracting the animal's attention. When a pencil is pointed at her through the wires of the cage she strikes at it with her right hand; the aim is true and sometimes she grasps the pencil and pulls it. Vision for objects (wires and rods) on both sides and from above and below is acute. A piece of potato was placed under a watch glass and introduced into the cage. The animal grabbed for it several successive times, then with both hands found the edges of the watch glass and made an attempt to turn it over. A piece of potato was placed in a small glass crystallizing dish, which the animal seized, turned over quickly but did not use the hand to secure the food but inserted the mouth. Another trial under similar conditions, but the potato dropped to the floor when the glass was introduced: the monkey picked up the dish, held it to the mouth and tried to get food from it leaving the food on the floor unnoticed. When the dish and the watch glass were placed in the cage she took up both even though no food was in them. Blocks of apple and carrot thrown into the cage are generally picked up quickly and accurately. Often she seems to look directly at a piece of food for some time before taking it up. She frequently misses a piece of food by 5 to 8 cm., and on groping gets farther off. With several different kinds of food thrown into the cage she does not appear to discriminate but picks up ginger snap along with the apple and only after having conveyed the ginger snap to the mouth does she reject it. She often picked at a knot hole in the floor of the cage and appeared to attempt to pick it up. Vision does not seem disturbed when tested by rods approached from the four retinal quadrants; the upper segment may have some dimness, for there is some inability to discriminate and to pick up food from the bottom of the cage. There is some incoördination of movement in prehension. It appears as if the animal does not discriminate between the colors, white, red, and brown." The last conclusion does not appear to me to follow from the results of the experiments, for although the animal in its normal condition took fruit in preference to bread and ginger snap both the latter kinds of food were eaten with apparent enjoyment. It also appears that

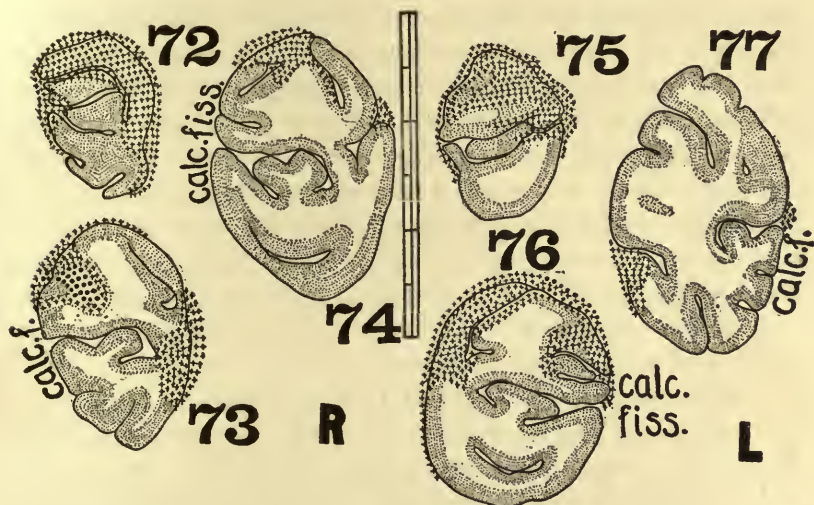
the incoördination of movement in grasping the particles of food may have given the impression that there is no ability to discriminate, for in tests with other animals it was found that when pieces of food were widely separated the movement was always made in the proper direction, although the food was not immediately secured, but that when the food pieces were close together the animal at times managed to get the wrong piece and often to take two pieces at once. It would perhaps be better to make a statement of the action rather than to draw the conclusion: the animal picked up indiscriminately pieces of white, brown and red food, although when these pieces were conveyed to the mouth only the red were usually eaten.



FIGS. 68, 69, 70 and 71. Monkey 6. Lateral and mesial aspects of the hemispheres, showing the extent of the lesion produced by cauterization of the pia and cortex. Slightly reduced. Traced from photographs.

The animal was killed two days later, without having shown any further variations in vision or other sensory functions. At the autopsy, the brain was found adherent to the dura and to the scalp over the site of the trephine buttons, and it was with diffi-

culty separated from the scalp. The brain weighed 94 grams. The occipital lobes were placed in alcohol for examination by the Nissl method and the remainder of the brain was hardened in bichromate for examination by the method of Donnagio.



FIGS. 72, 73, 74, 75, 76 and 77. Monkey 6. Frontal sections of cerebral hemispheres, with drawings of the histological examination. Slightly enlarged. Edinger drawing apparatus.

The results of the operation are to be found represented in figures 68 to 77. It will be seen that in this animal the cortex surrounding the calcarine fissure has not been disturbed to any extent and that the destruction of the visual cortex beyond the calcarine region has been very extensive. Such a lesion should have produced a very decided visual defect if this area were concerned with perceptions or sensations of a visual character, for with the exception of the cortex along the calcarine fissure practically all the so-called visual cortex has been affected.

The report of Dr. Lafora on the examination of the microscopical sections is as follows: "Monkey 6. Cauterization of the brain, frontal sections, Nissl method. On the left side the cortex along the calcarine fissure is not affected excepting the oral side of the superior ramification, at the extreme end of the occipital lobe. The lesion on the right closely corresponds with

that on the left, but there is a slight hemorrhage near the calcarine fissure." The examination by the method of Donnagio has not yet been completed.

Monkey 7. This animal was trained to discriminate the four colors. At first the animal did not seem to discriminate between the bitter breads, and for the first eight days of the experiments ate the bitter (green and yellow) breads, as well as the sweet (red and blue), even though at times the green and yellow were rolled in quinine and the animal had previously been thoroughly fed and the cheek pouches were filled with food. Oct. 27, the eighth day of the experiments, she refused the green and yellow breads most of the time, and on the following three days did not take the bitter breads once. On Nov. 1 and 3, she took the green bread once each day, but in later tests (November 5, 20, 25, and 28), after intervals of one, fourteen, four and two days, respectively, she made no mistakes.

The operation was performed Nov. 28. Both occipitals were cut away by a frontal incision. On cutting the left occipital, the right eye was observed to rotate slowly upwards and to the right, and this movement appeared to be concomitant with the slow drawing movement of the knife. The monkey reacted well after the operation, and two hours after having been placed in her cage was noticed to be busily engaged examining all parts of it. Her movements were rather slow, but they seemed to be executed well and precisely. No reaction to noises, loud or soft, e. g., whistling, clapping hands, etc., was observed, but anything moving about the cage attracted her attention. The observation cage had been placed in a room to which the animal was not accustomed, and she repeatedly went to the 5 cm. opening at the back and peered through it. Eight hours later the animal was found asleep, but when awakened seemed to be in the same state as that just described, curiously examining all things, following with the head and eyes moving objects, etc.

One day after the operation, a few tests with colored breads were made. In these the animal selected the red and blue and disregarded the green and yellow, but in each test did not take both sweet pieces. The movements were quick and accurate. She picked up food from the floor of the cage, accurately reached

up to the top of the cage and secured small pieces of sugar and other food which were held there. She was tested with the colored breads with the same result noted above. She was then placed in the cage with the male Monkey 8, whom she picked over for fleas, dandruff, etc., in a perfectly normal manner. During this procedure she was seen to stop, and make a quick movement, thereby catching a fly.

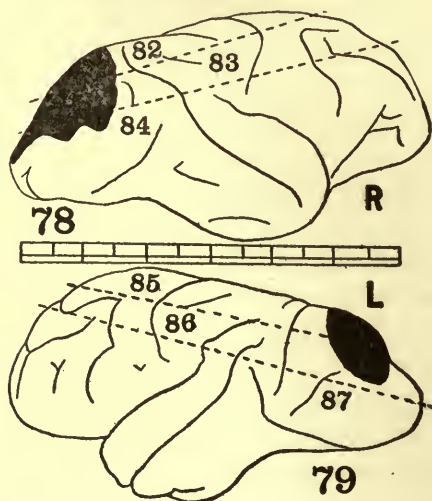
Two days after the operation (Nov. 30), ten tests with the colored breads showed perfect retention of the ability to discriminate, and on the following day (Dec. 1) the following results were obtained: Tests 1-6, ate all four pieces; 7, ate the red, blue and yellow, and disregarded the green; 8, ate red, blue and yellow, but did not pick up the green; 9, and 10, ate the red and blue, but did not take the yellow and green. Two days later she took red and blue in the first trial but refused to take more, and on the following day (Dec. 4) refused to work. Two days later in ten trials she ate all four pieces presented to her.

During the succeeding days no abnormality of vision was detected; the movements of grasping objects presented in any part of the visual field were accurate and quick, and there were no observable errors in discrimination. A second operation was determined upon but deferred for about four months and a half (April 16). During the intervening period the monkey was returned to the large cage with a normal monkey, and so far as it was observed acted in a perfectly normal manner. At the end of about four months the memory for the colored breads was tested and found to be defective. On the first day after this second series (March 29), she took all four pieces in the five tests, but two days later made only two mistakes in ten trials. During the next two weeks the monkey was given tests on three days, with intervals of 5 and 7 days respectively, in all of which the green and yellow were disregarded and the red and blue were taken. On the day of the second operation (April 16) the monkey took the yellow bread several times and the green once in ten trials.

Second operation, April 16. At the operation the posterior portions of the occipital cortex were cauterized. The site of the trephine openings made at the time of the first operation

were distinctly visible, the button on the right side was soft, that on the left was hard. New openings were made slightly posterior to these, and the old buttons were removed. It was found that the bridge of bone between the two original trephine openings had disappeared, so that when the new trephine holes were made, both occipitals were exposed and the bone opening extended from one side to the other. The loss of blood at the operation was slight and the animal recovered from the anesthetic soon after being taken from the operating table.

Fifteen minutes after the operation the monkey sat up in the

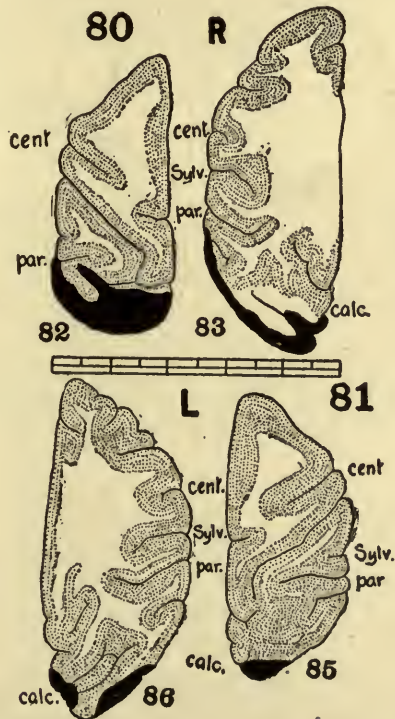


FIGS. 78 and 79. Monkey 7. Lateral aspects of cerebral hemispheres, showing the extent of lesions produced at the second operation, and the location of parts examined by histological methods. Slightly reduced. Traced from photographs.

cage, looked about in a dazed manner and moved about slowly. An hour after the operation she was more nearly normal. She took a piece of bread presented to her through the wire netting, moving forward about 25 cm. and reached for the food with an error of only about 3 cm. One hour later she was given a peanut, which she reached for accurately. She conveyed the peanut to her mouth, took the nut out of the shell and began to strip the red skin from the nut in a normal manner. When the shell

had been thrown away, the monkey took the nut from her mouth from time to time when stripping the skin from it and examined it until the skin had been removed. She was given water in a saucer, but did not drink it for an hour.

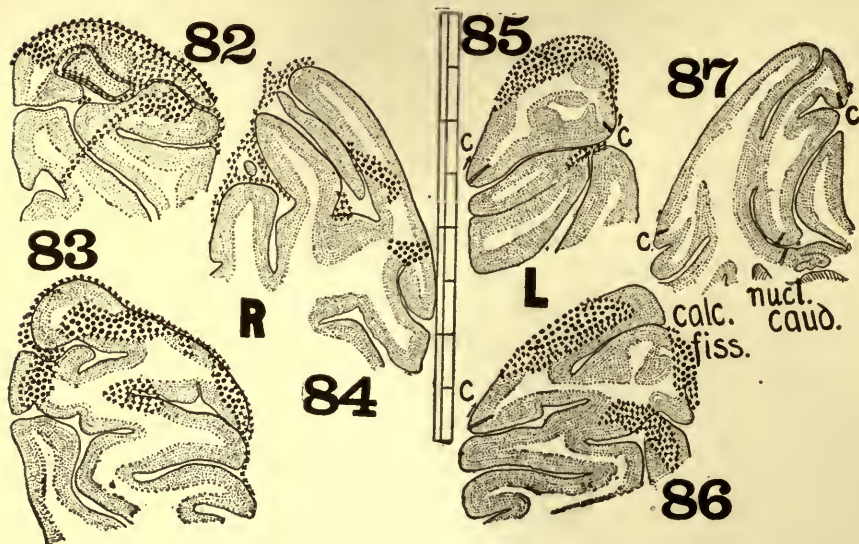
The day following the operation, the animal appeared to be normal, and two days after the operation in five tests with colored breads she showed perfect discrimination. At no time was there evidence of a visual disturbance as the result of this operation. The monkey was taken to Baltimore, April 20, and exhibited at the meeting of experimental psychologists, after which it was killed.



FIGS. 80 and 81. Monkey 7. Tracings from photographs of lower parts of sections 82, 83, 85, and 86, of figs. 78 and 79, showing extent of lesions. Slightly reduced.

At the autopsy the areas of softening of the cortex were distinctly noticeable apparently extending over the convexity of the

occipital lobes almost to the parieto-occipital fissure. The results of the autopsy and histological examinations are shown in the accompanying figures (78 to 87). In these it will be seen that the occipital poles have been almost entirely destroyed, and that the destruction of the so-called visuo-sensory cortex is extreme,



FIGS. 82, 83, 84, 85, 86 and 87. Monkey 7. Horizontal sections of cerebral hemispheres, with results of histological examinations, showing the amount of destruction by cauterization. Slightly enlarged. Edinger drawing apparatus.

with the exception of that surrounding the calcarine fissure.

The report of Dr. Lafora on the brain is as follows:

"Monkey 7. Cauterization of the brain: Nissl method; horizontal sections. On the right side the calcarine area is affected only at the superior branch of the fissure, but the cortex at the occipital pole is almost entirely destroyed. On the left side there is a marked destruction of the most posterior part of the occipital pole with an irritation lesion of the pia around this lesion. In the superior branch of the calcarine fissure there are some lesions." The effects of the first operation (section) were not determined by the histological method employed, and at the time of writing no examination of fibres had been made.

Monkey 8. This animal was trained to discriminate red and yellow breads. The training began Oct. 20 and continued until Nov. 26, with intervals of 2, 6, and 11 days—after the habit had been formed. At the latter date, the animal had indicated the ability to discriminate the red from the yellow, and to retain this over a period of eleven days.

The operation of cutting both occipitals was performed Nov. 26. There was considerable hemorrhage which was controlled by hot compresses. There was also considerable shock from the operation, and the monkey did not recover from the general defects for several hours. Immediately after the operation it was noted that the pupils were slightly dilated, but were equal. A slight nystagmus was suspected but at times this did not appear to be present, and it was impossible to decide whether or not the movement was partly voluntary. The eyes appeared to be rotated toward the right. When placed in the observation cage the animal was laid on the left side but it kept its head raised from the floor, and there was a slight tremor of the head. Three hours after the operation the animal appeared lethargic, its general movements were slow and apparently performed only with great effort and without much force. When a stick was thrust through the wire netting the monkey reached for it slowly but accurately. It grasped the stick, carried it toward its mouth and bit it, making these movements slowly and pulling and biting the stick without any display of energy. The wound or the bandage was apparently irritating, for the monkey continually scratched at the bandage when its attention was not attracted by and directed to objects held by the experimenter. The animal grasped food accurately but slowly, and picked up food which was placed on the floor of the cage, even when at the farther end (about 75 cm. distance). When a prune was held 10 cm. in front of the cage, the monkey put its hand through the mesh of the wire netting slowly but accurately, grasped the prune, drew it in, and immediately ate it.

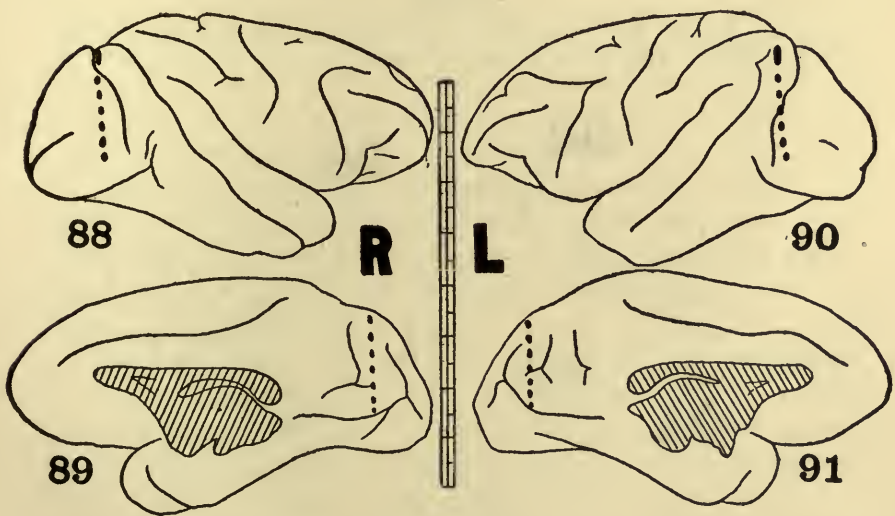
By the following day the dilation of pupils and the nystagmus (suspected) had disappeared. The general movements were more quickly performed, and the accuracy was the same as that following the operation. General tests with food were made, the

animal reacting in a normal manner, selecting pieces of food from a number placed on the floor of the cage, and rejecting those things which were of no value, and also those which it was known not to prefer, e. g., plain bread. No special tests of color were made on this day.

Two days after the operation the animal appeared able to see and to discriminate all kinds of food and other objects held in any part of the visual field, but when tested with the colored breads (which experiment was performed first on this day when the animal was hungry), the animal reached for and took both kinds of bread. It appeared at this time that the animal had lost the ability to discriminate the colors red and yellow in the bread test, although when tested with other foods of similar color (carrot, tomato, yellow turnip), there was no hesitation in selecting the red (tomato) and of selecting these vegetables instead of the red and yellow breads.

No special tests were made on the following day—the animal appearing to be in the same condition as that just mentioned. However, on the following day, four days after the operation, the animal was first tested with foods placed in different parts of the cage, with foods held in different visual segments and with foods outside the cage, the animal reacting at all times fairly quickly and accurately and at no time making errors in adjustment of more than one cm. After these tests (the monkey being not absolutely hungry) the tests with colored bread were made, and in the ten trials the monkey did not select the yellow bread once, and took only the red. It appears likely, therefore, that the errors made on the second day following the operation may have been due to hunger, any food being preferable to the animal than no food. The results of this test are particularly instructive, especially when they are considered in conjunction with the results of the similar tests with Monkey 7. With Monkey 7, it will be remembered (page 91), the animal discriminated the colored breads perfectly on the second day after the operation, but on the third day it appeared to have lost the ability. The latter result, in my opinion, is to be explained as due to the fact that these tests were performed at the beginning of the series of observations on that day, when the monkey had

not been fed for 24 hours, and when it was very hungry. A similar conclusion was drawn by me in regard to the monkey now under consideration. In the first tests of discrimination retention, the experiments were performed after a period of food abstinence, and the conclusion is drawn that the taking of both foods at this time was due to the extreme hunger of the animal. That this conclusion (or a similar one) is correct is evidenced by the fact that the discrimination of the breads on the fourth day following the operation was perfect from the first trial, and there was no mistake, not even that of touching the yellow pieces of bread. On the succeeding days the discrimination was perfect. The animal was killed eight days after the operation to determine the pathological condition.

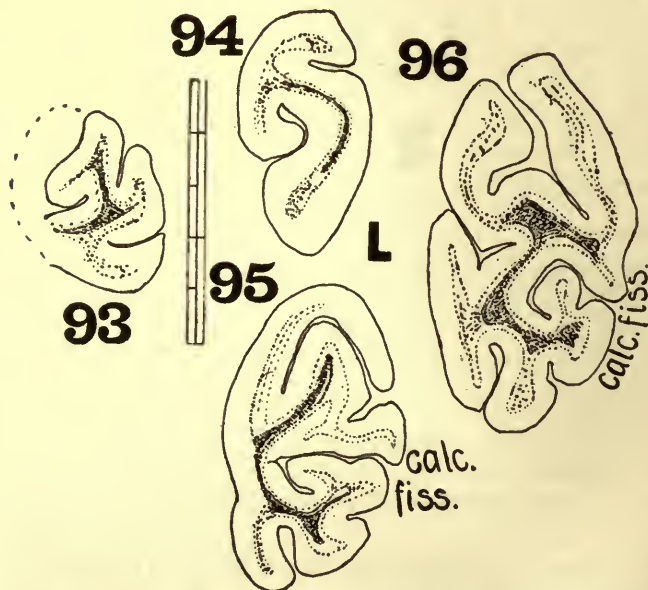


FIGS. 88, 89, 90 and 91. Monkey 8. Lateral and mesial aspects of the hemispheres, showing the course of the knife cuts and indicating the approximate extents of the lesions. Made from photographs. Slightly reduced.

At the autopsy, the brain was found to be in a healthy condition. The positions of the insertion of the knife into the hemispheres were visible, and it appeared that the knife had separated most of the occipital (visuo-sensory) lobe from the anterior part of the brain. The appearance of the brain is shown in figs. 88 to



FIG. 92. Monkey 8. Gross appearance through part of one section of the left hemisphere. Free hand, slightly enlarged.



FIGS. 93, 94, 95 and 96. Monkey 8. Microscopical appearance of frontal sections, showing degenerations as indicated by the method of Marchi. On the right side only part of one section was preserved, which probably corresponds with section 95 on the left. Edinger drawing apparatus, slightly enlarged.

91, in which are indicated the general courses of the knife cuts. The brain weighed 107 grams.

The brain was prepared for examination by the Marchi method to show the fiber degenerations, and at the time of the autopsy a drawing was made of one of the gross sections on the left side, in which there appeared to be an extensive hemorrhage. This is shown in fig. 92. At the time of the autopsy the right side was cut in the same way as the left, but none of the sections showed the appearance indicated on the left. After hardening, however, each of the three sections on the right was again divided and an appearance similar to that on the left was found on this side. In gross section the hemorrhage on the right side appeared to be more extensive than that on the left, including practically all of the white matter. At this time no sketch was made of the extent of the lesion on the right side, and this is especially unfortunate on account of the later accidental destruction of most of the posterior portions of this hemisphere. In the process of hardening and infiltration, all of the pieces of the right hemispheres, with the exception of part of one, disintegrated in the celloidin, leaving a muddy residue and this part of the brain was, therefore, not examined histologically. The part of the right side which did not disintegrate probably corresponds with section 95 on the left side, although this is not certain because so much has been lost.

Following is the report of Dr. Lafora on the microscopical findings: "Monkey 8. Section of the white substance, Marchi method by Dr. Achúcarro. On the left side the degeneration is not very well marked because of the short time the animal was permitted to live after the operation (eight days). Many fat drops, however, are observed in the sections, and they are more abundant in the *radiatio optica*, and in the *fasculus longitudinalis inferior*. In the white substance near the cortex many fat drops were also observed. From the study of the degenerated fibers, it is not certain that all the optical fibers on this side have been destroyed, but that many, perhaps most, have been affected by the degeneration, there can be no doubt. The section on the right side shows about the same degree of degeneration as those on the left, and although none of the parts can be accurately dis-

tinguished, it appears that this section corresponds with 95 on the left side."

The report of Dr. Lafora indicates a marked destruction of fibers on the left side which corresponds closely with what is to be expected from the extent of the hemorrhages indicated in figure 92. It is especially unfortunate that in this case the hemorrhagic appearance on the right side was not drawn and that the pieces of this hemisphere disintegrated and prevented a careful histological examination. Sufficient is shown in the part of the right side to show the marked degree of degeneration and to indicate an amount of destruction of fibers (fatty degeneration) corresponding with that on the left.

DISCUSSION OF RESULTS

The observations recorded in the foregoing pages show that destruction of parts of the so-called visuo-sensory cortex is accompanied by derangements of a varied character, but of minor degree when compared with those recorded by most previous investigators. Only one animal showed the marked visual disturbances which are comparable with those which have been reported by Munk, by Ferrier, by Schäfer and by others, and in this case the amount of destruction was much greater than in any other animal, and the disturbance did not become marked for some days after the operation.

The effects of the operations on the animals may be grouped into four general classes: the general appearance of the eyes and the ability of the eyes to move, the fields of vision, the discrimination of objects and of colors, and the ability of visual-motor coördination. In no case were all of these elements affected, and in most of the animals, as has been noted, the amount of disturbance was slight and was often limited to one of the elements just enumerated.

Some of the animals showed pupillary disturbances immediately after the operation. Three (monkeys 1, 2, and 8) had dilated pupils, but it is not possible to say definitely whether this condition was due to the effects of the operation as such or to the anesthetic. It is well known that following operations on

other parts of the body there may be pupillary disturbances, and these have been taken to indicate the effects of the anesthetic. In these monkeys we are also justified in concluding that the dilation is the effect of the anesthetic, although in one case it must be remembered that the pupils were not equally dilated. In the case just mentioned the left pupil was decidedly larger than the right, and this may have been a sequel of the operation, although it is not possible to determine this with exactitude. The fact that the other four animals did not show pupillary disturbances would lead me to suppose that in the cases of monkeys 1, 2, and 8 we had to deal with a chance condition, not with one intimately associated with the destruction of the occipital cortex.

It may be different, however, with the other eye movements. Immediately after the operation monkey 2 showed a tremor of the eyelids, and this was not the effect of the anesthetic, but an effect undoubtedly due to the operation on the occipitals. After the second operation on monkey 1, I observed that its eyes were turned inwards and upwards, and after the operation on monkey 8 the eyes were directed toward the right. In addition, monkey 8 showed a nystagmus following the operation, this condition persisting for some time. It was also observed that at the time of the operation on monkey 7, the occipital lobe being cut in this operation, the right eye slowly rotated upwards and turned toward the right at the time the section was being made.

These oculomotor disturbances were noticeable in only four of the animals upon which operations were performed, and it can not be concluded that they have a direct bearing upon the problem of the functions of this area. It is known that stimulation of the occipital lobes produces movements of the eye balls and of the intrinsic eye muscles, and it is possible that the motor defects are due to the destruction of the mechanism which, by its activity, produces corresponding movements. That the defects persisted for only a few hours or a few days indicates however, that the phenomena are due to an irritation rather than to a paralyzing effect, and it is pertinent to consider the slow upward rotation of the eye in monkey 7 at the time of the section as evidence of this. This condition corresponds with what has been found by

some investigators upon stimulation of the occipital cortex, and since it corresponds also with the more lasting (although transitory) effects in monkeys 1 and 8, it is at present justifiable to conclude that it is an irritative effect.

The general statement may be made that the operations did not produce any alteration in the ability of the animals to discriminate objects, for in all cases the animals were able to select food and to pick over the floor of the cage for objects which were later conveyed to their mouths. In only one case was there any difficulty, and this animal did not show this difficulty immediately after the operation, but only after a week. That all the animals which had previously been trained to discriminate colored breads were able to discriminate them after the operation is evident from the records of the individual cases. It was unfortunate that the tests of color vision after the operation could not be performed in exactly the same way as they were performed before the operation, but the results which were obtained with the new methods speak plainly for the retention of the color discrimination. In most of the cases the color tests were delayed for at least two days following the operation, so that any general shock effects of the operation might pass away and so that the animal should be in as normal a condition as possible for the tests. Even with this amount of time it was sometimes found that the animal would not take the colored breads, and the tests had to be made on a succeeding day. Monkey 1 discriminated the colored breads two days after the first operation, and three days after the second operation. Monkey 2 discriminated the colored breads three days after the operation. Monkey 4 discriminated the colored breads two days after the operation; monkey 5 did not work well during the first few days after the operation, but showed color discrimination ability on the sixth day, and similarly with monkey 6. Monkey 8 discriminated the colored breads on the fourth day, and monkey 7 was tested on the same days as the operations (two of which were performed on this animal) and both times was able to select the proper colors. From these results it can not be doubted that the ability to discriminate colors remained after the extensive operations which were performed, and it appears plain that the parts of

the brain which were destroyed have not the function of color perception or of color discrimination.

In addition to the special color tests, general tests were made with each animal, and the results of these general tests are in agreement with the special tests of color which were made with the breads. Even immediately after the operation, if the animal was sufficiently recovered from the effects of the anesthetic, there remained a marked ability to discriminate colored foods, and in most cases the judgment of the animal was unerring. When cotton wool, rolled into balls, was introduced into the cages, the animals at times picked up this material and placed it in the mouth, but this is exactly what a normal monkey does, and the fact is not evidence of a lack of color discrimination or a lack of discrimination of different foods. The selection of the pieces of melon which in color closely resembled some of the green pieces of bread, but did not resemble them in texture (the visual quality of which is uncertain), the selection of tomato instead of the red bread, and the selection of different foods from each other, as shown particularly in the accounts of the actions of monkeys 3, 4, 6, and 8, all indicate that the visual discrimination of these animals remained approximately normal. That the discrimination ability was not alone that of color is shown by the results with monkey 3, which had been trained to discriminate different sizes. This animal, it will be recalled, retained this ability after the operation, and it can not be taken as evidence other than that for the retention of the general ability of visual discrimination.

It would have taken too long a time to detail for each animal all the observations which indicated the normal amount of discrimination ability, but in addition to the observations which have been recorded above, and others which have been contained in the individual case histories, it may be well to indicate a few other facts which were observed. Whenever the door of the observation cage was opened the animal immediately walked out. In only one case was this discrimination ability disturbed, in monkey 5, and this animal showed at the same time an almost total loss of visual ability. When the operated animal was introduced into a cage with a normal animal it immediately walked

over to the second animal, picked him or her over for dandruff, and acted exactly like a normal unoperated monkey. In some cases when a male operated animal had been introduced into a cage with a female normal animal, he immediately mounted the female for sexual congress. It was found possible to fool an animal once or twice with cotton wool, but not more than this number of times, and this fact indicates either the retention of the discrimination ability it previously had or the retention of the general ability to learn very rapidly to discriminate particular objects. Whichever conclusion is considered correct makes little difference, for both indicate a high degree of discrimination ability. When food wrapped in papers or small wads of paper were introduced into the cages, the operated animals did not place the covered food or the wads of paper into the mouth, but pulled away the paper from the food, or pulled apart the wad of paper. In both cases there was a discrimination of the paper from food, for it was the habit of the animals to place food immediately into the mouth. When water was placed in the cages, most of the animals immediately stooped down to the dish and drank. In this experiment there must have been the retention of a visuo-motor habit, comprised of visual discrimination of the dish and the movements of the body, or there must have been a very great ability to discriminate slight degrees of variation of visual intensities or qualities. The threatening of strangers, a common trick with these monkeys, was shown in almost every case, a fact which also leads to the conclusion that there was an ability to discriminate me from the other observers who came to see them after the operations.

Some of the facts which have been cited above may also be explained in another way, viz., that the discrimination took place not because of a visual discrimination ability, but because of a smell discrimination ability. This might apply to the threatening attitude and to the behavior with another animal, but it can not be stretched to include all the observations which have been recorded. On the other hand, it may be said that the smell component in monkey life is not as great as in the carnivora, and that these animals depend much more upon vision and upon hearing. Smell ability may be taken to explain the ability to

perform a certain isolated act, but it can scarcely be taken to explain the ability of the animal to select unerringly five pieces of melon or of pear from among a large number of other pieces of food, since the animal did not place its nose near the food but selected the food apparently by eye and hand.

The observations regarding the visual fields are with the exception of those on monkey 5 consistent. No constriction of the field was found immediately after the operation in monkeys 1 (after two operations), 2, 3, 4, 6, 7 (two operations), and 8. In some of these animals there was what might have been taken by a casual observer to be a constriction of the field, but in the two monkeys in which such a defect was noticed, it was shown by careful tests to be something different from a constriction of the field. Monkey 3 showed a condition which has been interpreted as a diminution in visual acuity, because the animal was able to select things in all fields but selected those in some of the fields more readily than those in others. Monkey 4 showed an inaccuracy in reaching for things held above and below the direct line, but here we are dealing with a complex condition rather than with a simple inability to see with a certain part of the retina. It will be remembered that monkey 6 showed a similar defect after six days, but that on the first few days after the operation there was nothing to indicate a variation in the field of vision.

The movement phenomena were similar in all the animals. The variations in movement are of two kinds, the time and the accuracy. After the first operation monkey 1 was slow and indecisive, and in grasping movements made errors of about 2.5 to 5 cm. Immediately after the second operation the animal was slow and awkward, the movements were deliberate and inaccurate, and in all these ways they were quite unlike those of a normal animal. Twenty-two hours after the operation on monkey 2, it was noted that the movements were inaccurate, the inaccuracy lasting for about three days. Monkey 3 made a number of unsuccessful attempts to grasp food which was presented to it, and for a number of days the adjustment was not like that of a normal animal. Monkey 4 was also inaccurate in the taking of food, and monkey 5 was more inaccurate than any of the other animals. The last named animal at first could reach food

within 30 cm. of its body with a fair degree of accuracy, but outside of this area the movements were slow and inaccurate. This animal eventually became blind, and the results must be considered apart from those of the other seven animals which retained their visual ability. All the other animals showed inaccuracies, slowings and apparent indecisions.

These movement disturbances were found only in the processes in which the eyes had to contribute. They were not found with the movements which were of a reflex type, they were not found for movements which did not require the coöperation of the eyes, and no paralyses or pareses of the eyes or of any of the body muscles could be determined.

At first glance it may appear that we are here dealing with a visual disturbance which is evidenced by the lack of adjustment between the visual sensations and the movements of the arms and hands in grasping, but a few words may be said upon this point. Simple movements, such as those of grasping for food, depend upon a number of factors, which for simplicity we may reduce to three—the sensory, the motor, and the associational. It is by the proper combination of these that movements are performed accurately and quickly. If by any means the connection is interfered with (in the diaschisis sense of von Monakow), the end result of the afferent stimulation shows an abnormality, which may vary from a slowness or an inaccuracy to an apparent motor loss. All movements depend upon two primary factors, the motor and the sensory. If one of the two primary factors be disturbed, the movement as a whole is affected. It makes no difference in a general way which of the two primary elements be affected, except that if the motor element be destroyed there results a total paralysis. With the incomplete destruction of the motor element and with the complete or incomplete destruction of the afferent or sensory element, the general effect may be the same, viz., an inaccuracy, a paresis, or a slowing in movement. In the case of the reflexes the elimination of the sensory element may even produce a complete loss, just as well as the total elimination of the motor element. In the present work, however, we have to deal with a motor disturbance, not with a motor loss, and it is apparent that the effects can not be considered off-hand

as purely motor, and on the other hand, we must not conclude too rapidly that the effects are purely visuo-sensory.

That the disturbances are not of a motor type is well shown by the fact that other movements of a similar character were not affected at the time of the operation. The movements of conveying food to the mouth were accurate and quick. They were exactly like those of a normal animal, as far as this could be determined, and there was no motor defect in any of the movements concerned with parts of the body other than those of the hands and arms. The movements of the head, of the eyes, and even those of the hands and arms, when the animal did not have to deal with the taking of food, and with other movements in which the visual apparatus was involved, were well executed, and were as quick as those of a normal animal. It was apparent that the motor disturbances were associated movement disturbances, and were those in which the eyes were involved.

Since the movements which were affected were those in which the eyes were concerned as one of the afferent factors, we must look to see whether or not this element (the eye) has been disturbed and has produced the motor derangement. We have, I think, the right to conclude that the skeletal muscles or the direct motor control of these muscles have not been disturbed, because movements which did not involve the visual element were executed well. On the other hand we also know that for the execution of an accurate movement the afferent elements are most important. Coördination and the production of accurate movements are brought about largely through the association of afferent impulses with the efferent, and in the coördination there are many afferent elements associated. In connection with the movements under discussion, the more important (possibly the sole) sensory elements are the visual (including the sensations or perception of eye movements) and the musculo-tactile. Several times in the case histories it was mentioned that animals which exhibited an incoördination showed this especially for movements of grasping objects at a distance from the body. When, for example, objects were rolled toward the animal or when the objects touched any part of the body, the animal made quick and accurate movements, with a degree of coördination

apparently normal. When, however, such objects touched the body and bounded away the objects were not accurately grasped, but the animal fumbled in the place on the floor where the food had been, and in many cases was not able to locate the object without great difficulty. At times, also, a monkey would give up trying to secure the food which in rolling had touched the body and had then bounded away, and it was evident that the actual coördination of movements which were made with the musculo-tactile element alone was not impaired but that the impairment was due to some other element. In the case of the animal which eventually became practically blind (monkey 5) although food which was held at a distance of about 10 to 15 cm. from the head of the animal was not accurately grasped, other food which touched the body or the body hairs was taken immediately and accurately. Observations similar to these were repeatedly made with all the animals, and in every case in which there was a marked degree of incoördination or of inaccuracy in adjustment when the food was held at a distance from the body, there was no inaccuracy and no incoördination when the food was held close to the body or when it was touching the body hairs.

We are justified in concluding, therefore, that the movement disturbances were due neither to a disturbance of the motor process (muscles and motor impulses) alone, nor to the lack of or to the disturbance in physiological connection between the motor impulses and the tactile and muscular sensations. In view of this conclusion we are forced to conclude that the disturbances were due to a nervous factor connected with the visual apparatus. Here there are two sensory elements which may have a part in the disturbance—the true visual and the movement. The retention of the ability of visual discrimination speaks against the view that the disturbance was due to a true visual disturbance, for we are unable to say that there has been in these cases any constant visual disturbance of the nature of an amblyopia, nor even of the nature of a lessened irritability (in the sense of Loeb). On the other hand, there is nothing distinctive in the results which absolutely excludes this factor, except that we have found none of the animals unable to distinguish dif-

ferent kinds of food which have had very similar color and light qualities. If this element were the important one, I should expect to find that the animals would not be able to distinguish one kind of food from another which has a similar color and a similar brightness. This discrimination of food was found to be intact in all animals, and the only observations which may be taken to negative this conclusion are those of Dr. Barnes (p. 86). With these conclusions of Dr. Barnes I do not agree, as I have indicated in the proper place. It appears to me unlikely that a lessened irritability (which must be shown by a lessened discrimination ability) should have been present in all the animals which showed the movement disturbances, for, as has been said, all the animals were able to distinguish one kind of food from another, and each animal made a selection of food when different kinds were presented simultaneously. If this factor be excluded, as I believe it should be from the evidence at hand, there remain only two elements which might have contributed to the disturbance. These elements are the sensations of the movements of accommodation (i. e., of the lens, etc.) in the focussing of the images on the retina, and the sensations arising from the movements of the extrinsic eye muscles. We have very indirect evidence of the part which the two afferent motor processes took in the disturbances in the monkeys. Observations were made of pupillary changes in some of the animals, and of pathological conditions of the extrinsic eye muscles, but none of the conditions was constant. We are unable to determine the sensory losses in these fields in animals, on account of the lack of information which the animal can give us, and on account of the inability to judge of the focussing and of accommodation abilities of the animal. The evidence is too general to exclude one of these factors and it appears to me that the only conclusion which, under the circumstances, is warranted is that the motor disturbances are due to the loss of or to defects in the sensational elements from the oculo-motor apparatus. That the eye ball movements and the movements of accommodation may remain normal even after the destruction of the corresponding cortical center is not unlikely, for we know that these movements are reflex, and are only affected in a general way by the activity of the cortex. If the corpora

quadrigemina remain intact the eye movements may remain almost normal, and they may be produced in such a way that the impression is obtained of complete and normal cortical control. This, I believe was the condition in the monkeys which I studied.

It is unfortunate that the work of Vitzou and that of Panici are not accompanied by illustrations of the extents of the lesions in the animals upon which they operated, for their physiological results have certain relations with the present work, which can not be discussed fully without the accurate description of the lesions. We do know enough, however, to be able to say that their results resemble those recorded in the foregoing paper to an extent unlike those of previous investigators with the possible exception of those of Ferrier. The accounts of Ferrier's monkeys with occipital lesions (see pp. 14-16) read much like those given by me and by the other observers who had an opportunity to study the animals carefully after the operations. It will be remembered that Ferrier's animals could see although the occipitals were extirpated, they ran away when they were approached, they avoided obstacles which were in their path, and one animal was able to see sufficiently well two hours after the operation to be able to pick up particles of food from the floor of the cage.

In view of the possibility of the establishment of new paths, possibly though lower centers, it is not surprising that Vitzou's animals were able to recover to a larger extent their visual ability, but it must not be understood that the recovery was complete, and in fact there is nothing in Vitzou's work to indicate the possibility of discrimination of a high degree. The fact that animals may relearn habits after the frontal lobes have been extirpated was interpreted by me to be due to the formation of new paths, and it appears to me most likely that Vitzou's animals also formed new paths for certain visuo-motor habits, even though the occipitals were destroyed.

The results obtained by Panici are most nearly like those recorded in the foregoing paper, but from the accounts of the animal activities it is impossible to determine how much of the visual functions, which he judged were retained, were retained because of the lower reflex connections, and how much real dis-

crimination ability was retained. The criticism of the work of Goltz applies here as well as it did to the original work, and it may be said again, as von Monakow has said, that the retention of simple eye movements, or even of simple visual-motor habits, etc., does not indicate whether or not there has been a retention of vision in the sense in which this term is properly used. There is undoubtedly a connection between the eyes and certain motor centers, but we are not able to say that discrimination has taken place, and without evidence of visual discrimination the interpretation that visual functions *per se* remain will not stand.

The consideration of the results recorded by me, with those which have been recorded by Ferrier, by Vitzou and by Panici, lead directly to the conclusion that previous investigators who have assigned to the occipitals a visual function have destroyed large portions of the lobe, and have been content to assign a visual function to its several parts as a whole without dividing it into individual elements. The conclusion is forced upon us that the lateral parts of the occipital lobes, which also have the calcarine type of cortex, have not a true visual function but a function in connection with the afferent impulses from the eye muscles. This, it will be noted, is not inconsistent with the results of previous investigators, although it is opposed to the conclusion that the whole occipital portion of the cerebrum is visual in function, and although it is opposed to the conclusion that in this portion there is a projection of the retina, such as Henschen believes.

SUMMARY AND CONCLUSIONS

The monkey readily learns to discriminate colors if the colors are parts of objects to which the animal attends.

Extirpation of the lateral parts of the occipital lobes does not interfere with color discrimination.

Extirpation of the lateral parts of the so-called visuo-sensory cortex in the monkey does not produce disturbances of a true visual character.

The destruction of the lateral parts of the occipital lobes is followed by disturbances in coördination of movements which are based upon the sensations from the eye and its appendages.

The disturbances in coördination are not due to a lack or to a loss of the true visual element, but to a lack or to a loss of the afferent motor elements, viz., those from the intrinsic or from the extrinsic eye muscles.

One animal in which the cortex surrounding the calcarine fissure was destroyed showed a true visual disturbance corresponding with those described in man.

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